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Some Competitive Relationships between *Agropyron spicatum* and *Bromus tectorum*

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# SOME COMPETITIVE RELATIONSHIPS BETWEEN *AGROPYRON SPICATUM* AND *BROMUS TECTORUM*

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## INTRODUCTION

In its pristine condition the vegetation of the northern intermountain region of the United States was in dynamic balance with its environment. Perennials were dominant with various life forms and wide floristic diversity represented. The relatively few large herbivores caused only minor disturbance to the vegetation, except perhaps locally. Though man was part of these ecosystems, his numbers were not great, and his society so primitive that he had little impact upon the vegetation. He had no domestic livestock and practiced very little crop agriculture. Fire was his most destructive tool.

*Agropyron spicatum* (Pursh) Scribn. & Smith (bluebunch wheatgrass) was the major plant species of this region. It flourished on open semiarid sites from the valleys of the Canadian Rockies south to the mountain ridges of Mexican Sonora, and from the slopes of the Cascade Mountains east to the short-grass plains. In the central part of the Columbia Plateau, and in other less extensive areas, this species was the dominant plant, producing more herbage than all other associated species combined (Daubenmire 1942, Table 4). Furthermore, it provided an important understory cover in association with shrubs and trees on millions of additional acres.

The introduction of European culture into this region with its traditional use of the plow, domestic livestock, exotic plants, and fire control, foreshadowed

destruction of the pristine ecologic balance forever. Largely through economic pressures and a general lack of understanding, intensified grazing resulted in widespread destruction of *A. spicatum* and an opportunity for weed invasion on a grand scale. None of the numerous indigenous annual weed species was of sufficient vigor to exclude all of the subsequently introduced annuals (Daubenmire 1942, p. 75). Thus, several annual species introduced from Europe and Asia have replaced perennial species.

*Bromus tectorum* L. (cheatgrass) invaded and dominated several million acres previously held by *A. spicatum*. This species is highly palatable in early spring, and produces excellent yields of forage in normal years. However, it is less desirable in many respects than perennial species which it has replaced.

As man has brought the land more and more completely under his control, he has become increasingly aware of some of the undesirable consequences of his past mismanagement. Serious attempts are now being made to restore valuable perennial forage species on native ranges by reducing grazing pressure or by artificial seeding. Both of these alternatives are expensive.

The basic factors controlling competitive relationships between perennials and annuals on our ranges must be thoroughly understood if more than trial and error attempts at restoration are to be made. It is the objective of the present study to increase such understanding.

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## REVIEW OF LITERATURE

### COMPETITION DEFINED

The term "competition," widely used in the literature of numerous disciplines, has many and varied meanings. In this paper, the definitions of Harper (1961) and Donald (1963) have been accepted. Harper defines competition as "the short- and long-term hardships which result to organisms from the proximity of neighbours except that it does not include the direct effect of parasites and predators upon their prey or hosts . . ." He further suggests that a new term, "interference" be used to specify the kind of competition experienced by plants growing near enough to undergo hardships. Donald agrees in principle with Harper's definition, but feels that the term "competition" is preferable if used in its original context, and as defined by Clements (1904). Donald's definition is as follows:

Competition occurs when each of two or more organisms seeks the measure it wants of any particular factor or thing and when the immediate supply of the factor or thing is below the combined demand of the organisms.

Much of the literature relating to competition deals with agricultural cropping, and the influence of cropping on yields (Donald 1963). In the present study, seedling survival, not yield, is emphasized.

### COMPETITION BETWEEN SUBJECT SPECIES

Ecologic relationships between *A. spicatum* and *B. tectorum* have been described extensively but largely as opinions based upon experience rather than formal research. Presumably, these writings are the outcome of half a century of concern by those who have been in direct contact with the problem of depletion in climax plant associations, followed by annual grass invasion.

Another segment of the literature is devoted to investigation of competitive relationships between mature established plants of *A. spicatum* and invading seedlings of annual grasses, particularly *B. tectorum*. Most reports on this problem agree that *B. tectorum* can, and does, invade climax stands dominated by *A. spicatum* in various parts of its range. Typical of these, Daubenmire (1942) relates that *B. tectorum* appears to be a fully naturalized alien in central Washington, presently found in the indigenous low herb synusia of the climax "*Agropyronetum*." Poulton (1955) reports 12% coverage for *B. tectorum* in a climatic climax *Agropyron-Poa* association in northern Oregon. Gooding (1957), Hulbert (1955), Pickford (1932), Stewart & Hull (1949), and Tisdale (1947) all report finding *B. tectorum* seedlings capable of competing, at least in

small numbers and depauperate form, with established climax stands of *A. spicatum*.

However, dominance of *B. tectorum* on *A. spicatum* sites is only known to occur as the result of disturbance such as overgrazing, fire, plowing, fertilizer application, or trampling. Biotic climax result after heavy overgrazing in eastern Washington (Daubenmire 1942). Young (1943) reported that with severe overgrazing, *Poa secunda* Presl. and *B. tectorum* became dominant on shallow soils near Moscow, Idaho, replacing *A. spicatum*. Taking the retrogression farther, Daubenmire (1940) observed that intensive spring sheep grazing destroyed a stand of *B. tectorum* by preventing its seed production. The cover was thus reduced to a group of low value, low-yielding annual forbs and grasses. Warg (1938) noted that *A. spicatum* exerts its greatest dominance on protected areas in western Montana, while *B. tectorum* exercises its greatest dominance on abandoned fields, overgrazed ranges, or repeatedly burned areas. Pickford (1932) found that, in Utah, fire reduced perennial grasses and *A. tridentata* while increasing *B. tectorum*. On the other hand, grazing reduced perennial grasses but increased *B. tectorum* and *A. tridentata*. Burning and grazing combined reduced overall density to one-quarter of climax cover by removal of most of the perennial grasses (primarily *A. spicatum*) and *A. tridentata*, but increased *B. tectorum*. Hanson & Stoddart (1940) also working in Utah, found that grazing reduced *A. spicatum* root weights in the soil profile to about one-sixth that produced on an undisturbed site, and that, to a large extent, *B. tectorum* replaced the former species under these conditions. Stoddart (1941) also described the invasion of *B. tectorum* on disturbed Palouse grassland areas found in northern Utah, while Stewart & Hull (1949) described the same phenomenon in southern Idaho.

Wilson, Harris & Gates (1966) report that applications of ammonium sulfate to near-climax *A. spicatum* stands in eastern Washington resulted in retrogressive succession, i.e. a large increase in *B. tectorum* yields at the expense of *A. spicatum* yields. Soil moisture, the usual limiting factor for late-maturing species, is not limiting during late fall to early spring when *B. tectorum* growth and reproduction occur.

Reestablishment of *A. spicatum* seedlings on sites relinquished to *B. tectorum* is another facet of the competition problem. In this situation both species are competing as seedlings; *A. spicatum* seedlings must be sufficiently competitive to become perennial if secondary succession is to lead back toward the original climax. In some regions, seedlings of other perennial grass species (of a developmental sere) may compete and become established directly in *B. tectorum* stands, and later these stands may be invaded by seedlings of *A. spicatum* (Piemeisel 1951).

The literature hints that regional variations exist in the relationship between these two species. Hitchcock (1950) implies that the climate of Washington and Oregon (presumably east of the Cascade Moun-



tains) more nearly meets the growth requirements of *B. tectorum* than any other region, despite its presence in almost every state. Daubenmire's work (1942) in eastern Washington seems to corroborate Hitchcock's inference. He reports that even after 30 yrs of protection from grazing and fire, *A. spicatum* seedlings have not invaded dense stands of *B. tectorum* on one site under observation. A series of abandoned fields was examined with Dr. Daubenmire on Page Creek, near Clarkston, Washington, which have been abandoned for up to 40 yrs. The surrounding native vegetation is typical of the *Agropyron-Poa* habitat type. Fields abandoned for 1 yr were dominated by *B. tectorum* as were fields abandoned for 40 yrs. No evidence could be found within the field or on field borders that *A. spicatum* plants were invading the area. Dr. Daubenmire believes that *B. tectorum* is able to maintain dominance on the area indefinitely.

Reports are available to indicate that elsewhere reinvasion is somewhat more rapid. Warg (1938), working in western Montana, reported establishment of *A. spicatum* seedlings in dense stands of *B. tectorum* around the edges of abandoned fields after 10 yrs, and estimated that perhaps 30 yrs would be required for reestablishment of dominance by *A. spicatum*. Over a 5-yr period (1939-1943), Tisdale (1947) recorded the reestablishment of *A. spicatum* seedlings on protected depleted ranges of British Columbia. Several others believe that grazing control is all that is needed to allow perennial grasses to replace *B. tectorum* as the dominant species (Leopold 1941; Hull & Peckance 1947; Pickford 1932; Piemeisel & Chamberlin 1936; U.S. Forest Service 1937). Some of these authors do not make clear however, whether the perennials return as seedlings or as enlarged remnants of old established plants.

Most investigators who have studied the problem of seeding perennial grasses into *B. tectorum* stands have eventually concluded that this annual provides very intensive competition to seedlings of perennial grasses. In most instances stands of *B. tectorum* have successfully resisted seeding attempts which have not included effective measures for its control. Robertson & Pearce (1945) treated it as a "closed community." They emphasized that whether the closed community is one of annuals or perennials is immaterial; the problem of successful establishment of perennial grass seedlings is essentially the same in either case. They hypothesize as to the critical nature of the competition involved as follows:

"By virtue of its vigorous spring growth, *B. tectorum* in dense stands draws heavily on the soil moisture provided by winter snows and spring rains by the time it matures seed. Moisture is then not adequate to sustain the slower growing perennial grass seedlings through the normally dry summer and fall. Any effective summer rains that occur after the *B. tectorum* plants have become dormant are available for perennials, and this may explain the successful reseeding in established *B. tectorum* in occasional years, or in regions with considerable summer rainfall."

More relevant to the present study, but fewer in number, are reports of research directly concerned with competition between the subject species. Using plants in gallon cans and others in glass-faced boxes in a greenhouse, Hull (1963) found that *B. tectorum* competition reduced the seedling top growth yields of *Agropyron desertorum* (Fisch.) Schult., *A. cristatum* (L.) Gaertn. and *A. sibiricum* (Willd.) Beauv. to between one-seventh and one-third of that produced without interspecific competition. Root growth was similarly reduced.

Warg (1938) set up a greenhouse experiment in which he planted 119 *A. spicatum* seeds and 100 *B. tectorum* seeds in the same pot to give equal numbers of seedlings per square foot. Leaf growth of *A. spicatum* slackened 7 days after the final irrigation, and ceased entirely at the end of 12 days. In contrast, *B. tectorum* seedling growth slackened after 10 days without water and ceased growth after 15 days. Permanent wilting of *A. spicatum* developed 20 days after the final irrigation, while *B. tectorum* seedlings survived for 24 days. He credited this longer survival to a superior ability in *B. tectorum* to extract moisture from the soil.

Evans (1961) grew 18 *A. desertorum* seedlings per greenhouse box (1 x 1 x 3 ft deep) in competition with various numbers of *B. tectorum* plants, from 0 to 256 per sq ft of soil surface. He found *A. desertorum* seedling growth affected in two ways by *B. tectorum* competition: (1) early leaf growth was slowed by increasing competition, and (2) cessation of growth occurred earlier with each increase in intensity of competition. Furthermore, shoot and root weights were inversely related to increases in *B. tectorum* densities. However, total *B. tectorum* yields increased with increasing numbers of that species. He interpreted the factors of competition to be (1) reduction of early leaf growth as a result of lowered light intensity, and (2) early cessation of growth at the end of the experiment as a result of decreased soil moisture.

Rummel (1946) working with shallow greenhouse boxes, found that in competition with dense stands of *B. tectorum* seedlings under adequate moisture levels, the number of *A. desertorum* seedlings surviving was reduced to about 50% and *Agropyron smithii* Rydb. seedlings to about 10% of the number on plots without *B. tectorum*. Competition also markedly reduced top and root weights, seedling leaf heights, and root lengths of both perennial species. He concluded that species which germinate early in the season and make rapid growth following emergence, as *A. desertorum* does, resist *B. tectorum* competition more successfully than slower developing species such as *A. smithii*. Adequate moisture levels produced heavy *B. tectorum* growth which limited light available to the competing species, and suppressed them.

#### STUDY SITES

Field studies reported here were primarily conducted at two locations, in addition to the laboratory



studies. Field competition, rooting depths, and soil moisture relationships were studied at the Harder Ranch in Adams County, Washington, where two 20-acre seedings of *A. spicatum* were available for use. In addition, root growth studies were conducted at the old Forest Nursery site at Pullman, Washington. A description of the general characteristics of these two sites is appropriate to an interpretation of the results.

#### HARDER RANCH

The Harder Ranch is located in Adams County near Benge, Washington. The experimental plots are located in the southwest quarter of Section 16, T 17 N, R 37 E, W.P.M., at an elevation of about 490 m above mean sea level. The topography of the plots is essentially level, with low buttes rising to heights of about 60 m in the vicinity. Geologically, the area is a portion of a glacial outwash plain, with alluvial materials of undetermined depth overlying basalt bedrock.

The surface structure, called "biscuit scabland," is typically comprised of mounds of deeper, stone-free soil of unknown origin appearing in a matrix of shallow, stony soil. The mounds are roughly circular on the ground surface, rising from 30 to 90 cm in height above the general land level. They vary from about 5 to 20 m in diameter. In cross section the soil body comprising the mound has a lens-like shape, set over the stony soil matrix. Approximately 10% of the study area is covered by these "biscuits." This structure is typical of large areas in eastern Washington and Oregon. The studies reported here were conducted entirely on the shallow phase as described below.

The soil has been classified as a medium-textured Benge series, chestnut great soil group. The parent material consists of alluvium from various sources, mainly basaltic, with some surface influence from wind deposited loess. The A horizon is a dark brown silt loam, 27 to 30 cm deep, with a few 12 to 50 cm (or sometimes larger) boulders scattered throughout. Structural peds are weakly evident. There is no indication of a B horizon, but the C horizon extends to about 65 cm, where it abruptly changes into a loose, open gravel deposit.

In its undisturbed condition the vegetation was the *Agropyron/Poa* association (Daubenmire 1942) commonly found as the climatic climax in this zone. At the beginning of the study, however, the general aspect of the dominant vegetation was a dense stand of *B. tectorum* with an understory of *Poa secunda* and scattered remnants of *A. spicatum*. There were also the usual scattered plants of *Chrysothamnus nauseosus* (Pall.) Britt. and numerous low annual grasses and forbs.

Average annual precipitation is approximately 30.5 cm; the distribution pattern is fall-winter-spring with dry summers. Temperature variation between summer and winter months is relatively narrow, averaging  $-2^{\circ}\text{C}$ . for January and  $24^{\circ}\text{C}$ . for July (coldest

and hottest months, respectively). These data reflect the oceanic influence expressed in this region.

Winter and summer temperatures are sufficiently extreme that when coupled with drought in summer and snow in winter, plants are more or less dormant during both of these seasons. Some deep-rooting plants such as *A. spicatum*, *Artemisia tridentata*, and *Chrysothamnus nauseosus* continue growth and reproductive activities into late summer but most species mature and lie dormant through June, July, and August each year. Some plants grow in winter, especially the root systems of certain annual species.

#### PULLMAN FOREST NURSERY

The old Pullman forest nursery is located on Washington State University campus. This area had been plowed and farmed since before the turn of the century, and in more recent years was used for the production of windbreak tree seedlings in the Clark-McNary reforestation program. Within the past 5 yrs the nursery has been a forestry and range management research site.

The research plots were located in the northeast quarter of Section 5, T 14N, R 45 E, W.P.M., at an elevation of 775 m above mean sea level. The plot area has gently rolling topography with a SW exposure. Geologically, the area is a portion of the Palouse Hills formation which has medium-textured loessal material of varying depths from a few centimeters to several hundred decimeters overlying basaltic bedrock.

The soil is Athena silt loam, a chernozem. In the plot location the Athena series tends to be transitional toward the Palouse series which holds a similar topographic relationship in the prairie catena under slightly higher precipitation. The A horizon is dark brown and extends to approximately 30 cm depth. The AB horizon, of similar silt loam texture, but yellowish-brown in color, extends to about 70 cm depth. The B horizon is light yellowish-brown silt loam, very friable and with coarse sub-angular blocky structure. At about 90 cm the  $B_{3ca}$  horizon has a cemented, practically impervious stratum high in calcium content.

In its undisturbed condition, the native vegetation of this site was dominated by the *Festuca/Symphoricarpos* association (Daubenmire 1942) which was commonly found as the climatic climax in this zone.

The climate at the nursery and Harder Ranch plots is very similar except that the average annual precipitation at Pullman is approximately 51 cm. The increased cloudiness necessary to produce the increased precipitation results in less sunshine, slightly cooler summers, and slightly warmer winters. January temperatures average  $-1^{\circ}\text{C}$ ., and July  $27^{\circ}\text{C}$ .

#### TAXONOMY AND LIFE HISTORY

##### AGROPYRON SPICATUM

The grasses of this study are both in the subfamily *Festucoideae*; *A. spicatum* is in the *Hordeae* tribe, and *B. tectorum* the *Festuceae* (Hitchcock 1950).



*Agropyron spicatum* has frequently been divided into two species by taxonomists. Hitchcock (1950) recognizes plants with divergently awned spikelets as *A. spicatum*, awnless individuals as *A. inerme* (Scribn. & Smith) Rydb. However, ecologists working with these plants in the field have expressed considerable dissatisfaction with Hitchcock's classification. Daubenmire (1939, 1960) points out that plants having all degrees of awns to awnlessness and of divergence in awns are found in the field. Hitchcock's description and classification ignores the intermediate short awns, as well as awns on some spikelets but none on others within the same spike. Daubenmire (1960) demonstrated that awn lengths intergrade completely from one extreme to the other, and concluded that awn length is an unsuitable characteristic upon which to base division of this material. Daubenmire (1939, 1960), Stoddart (1941), Passey & Hugie (1963), and others have noted that *A. spicatum* and especially *A. inerme* frequently have rhizomes, contrary to Hitchcock's description.

Daubenmire (1960) concludes that:

"Segregation of these biotypes in the field appears to be a result of habitat selection that allows rhizomatous individuals to prosper in less arid grassland, whereas only caespitose individuals survive in the more arid grassland and semi-desert. In eastern Washington and northern Idaho early stages of succession favor the caespitose biotype, but where aridity is not intense, the subsequent development of a dense vegetative cover results in a replacement of caespitose pioneers by rhizomatous plants, so that the two ecotypes have both a time and a space sequence."

Daubenmire (1960) finally concludes that since *A. inerme* is distinguished from *A. spicatum* only on the basis of its awnless character, and this character intergrades completely, and since the caespitose-rhizomatous character cuts across both these groups, all plants should be grouped under the name *A. spicatum*. He further proposes that the description be enlarged to cover the entire group of awnless to divergently awned and caespitose to rhizomatous plants.

Experience has led to acceptance of Daubenmire's proposal. In this paper the name *A. spicatum* will include Hitchcock's *A. spicatum* and *A. inerme* as well as the unnamed material which intergrades between these two. Pressed specimens of the ecotypes used in this study may be examined in the Range Management Herbarium at Washington State University.

In recognition of tremendous genecological variation which occurs in a taxon as widely distributed geographically as *A. spicatum*, a genetically uniform ecotype was sought for use in competition tests conducted in this study. It was found in an agronomic selection of the native species used widely in conservation plantings by the Soil Conservation Service, U.S. Department of Agriculture (Hafenrichter, Mullen & Brown 1941). This selection has been named "Whitmar," an awnless, rhizomatous ecotype. It has been tested widely throughout the Pacific

Northwest, and found to produce heavily even in relation to local ecotypes on droughty sites. Unless otherwise indicated, all experimental results reported for *A. spicatum* relate to the Whitmar selection. Seed was supplied by the Soil Conservation Service, Plant Materials Center, Pullman, Washington.

Leaf growth on mature plants normally begins in September or October when increased soil moisture and cool growing temperatures coincide. The leaves grow only slightly during winter, but may be 12-15 cm tall when spring snows melt. The appearance of the inflorescence in the boot stage usually begins in early June and the reproductive stage ends in summer dormancy by mid-July. In some unusual seasons most of the plants may fail entirely to produce seed culms, remaining in the vegetative stage until summer dormancy. A complete description appears in the Range Plant Handbook (U.S. Forest Service 1937).

Although *A. spicatum* is one of the major forage plants over large areas of the west, much care must be exercised in grazing management if it is maintained in the stand. The upright stature of the plant, makes it vulnerable to overuse (Fig. 4). It is particularly sensitive to grazing during its reproductive phases.

#### BROMUS TECTORUM

The taxonomy of *B. tectorum* is very straightforward. Since Linnaeus named the species in 1753 there have been no nomenclatural changes.

However, following the methods of Turesson (1922) and Clauson, Keck & Hiesey (1939), geographic races of *B. tectorum* were brought together in a garden at Lewiston, Idaho, where Hulbert (1955) demonstrated the existence of several distinct ecotypes. He noted important differences in winter hardiness, phenology, height of culms, pubescence on lemmas, openness of panicles, and dorsal compression of florets among the plantings.

To optimize uniform response from *B. tectorum* in these competition studies, the seed used has been collected annually from a single location at the Harder Ranch experimental site.

*B. tectorum* is an annual with considerable plasticity in its responses to variations in site. It may produce a single culm 5 to 10 cm tall bearing one spikelet when growing in a very dense monospecific stand, or on a sterile, droughty site. On the other hand, where soil moisture, fertility or light intensity are not limiting, an individual plant may produce 12 to 15 or more culms, each 50 to 75 cm tall and bearing hundreds of spikelets per culm (Fig. 1). Yield of forage varies as much as 1,000% from year to year, making hazardous any grazing operation based solely on this species (Hull 1949). Its yields in normal years are usually comparable to, or in excess of, perennial grass yields on similar sites. When the forage is succulent it has high nutrient and preference value with both sheep and cattle.



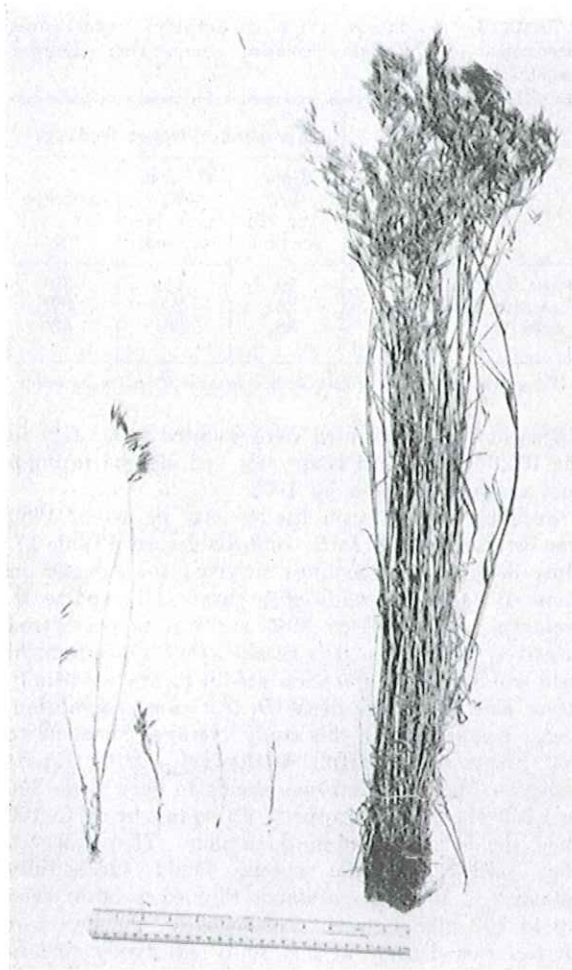


FIG. 1. *Bromus tectorum* plants grown at Harder Ranch site, 1962, indicating growth response to varying site conditions.

*B. tectorum* leaves grow but little in the fall, usually averaging 2 to 4 cm tall when covered by snow in December. It does not reach grazing height for cattle in the spring until 2 to 3 weeks later than most associated perennial grass species. Once growth begins the reproductive cycle is rapidly completed and the plant dies, usually by late May. After reaching maturity, *B. tectorum* forage becomes unpalatable and low in nutrient value. In this condition it presents a serious fire hazard, and furthermore, the sharp-callused seeds may cause blindness and lumpy jaw (actinomycosis) in grazing animals as the result of puncture wounds. Several good descriptions of *B. tectorum* are found in the literature (Klenmedson & Smith 1964; Stewart & Hull 1949).

Under most conditions *B. tectorum* is a winter annual. But several plants of this species have been observed in the field to persist through two winters and the intervening summer. During the spring and summer of 1959 a field-sized plot was summer-fallowed at the Harder Ranch site, killing most of the *B. tectorum* as well as other annuals and perennials.

In the fall of 1959 a few scattered plants of *B. tectorum* germinated and produced seed in the spring of 1960. In mid-July 1960 a number of these same *B. tectorum* plants were green and producing a second set of tillers which subsequently produced seed. All such observed plants were growing on the deep "biscuit" soils where moisture content was relatively high, likely due to the previous year of fallow and the scattered distribution of the *B. tectorum*. Ten individual plants were marked for future identification. Eight of these were observed to produce a third set of tillers in the fall of 1960, and these matured into inflorescences in the spring of 1961. All of these plants succumbed with the onset of the normal 1961 summer dry period, and intense competition.

Production of two successive sets of inflorescences in a single growing season is fairly common. In the spring of 1964, for example, *B. tectorum* at the Harder Ranch site produced inflorescences averaging 10 to 12 cm tall during the unusually dry spring season. Then, as the spring season seemed about to terminate, a series of unusual summer storms moistened the soil surface; subsequently the drying plants revived and produced, a second, taller set of flowering stems. A similar response was observed in western Montana in the summer of 1959.

Warg (1938) states that *B. tectorum* was probably introduced into east coast states before it was known in the west. It may have migrated across the continent, or it was introduced directly into the west from the Mediterranean region. He cites Alphonso Wood's 1861 edition of the "Classical Book of Botany" as the first to list *B. tectorum* in the United States and notes that the earliest known collection in the west was made in 1893 by Sandberg and Lieberg in Washington. However, the plant must have been widely scattered throughout the west at this time because successive collections were made in such widely separated places as Utah in 1894 by Marcus E. Jones, Colorado in 1895 by C. S. Crandall, and Wyoming in 1900 by Aven Nelson (Hulbert 1955).

At the present time *B. tectorum* occurs in all states of the U.S. except those in the extreme southeast. However, its best adaptation is in the Pacific Northwest.

#### FIELD COMPETITION

A 20-acre field at the Harder Ranch site was drilled to 7 lb of *A. spicatum* seed per acre in October 1959. The site had been sprayed for control of *B. tectorum* early in the spring of 1959. This treatment was successful where applied, but many strips were unintentionally left unsprayed between consecutive spray boom passes. An attempt was made to control *B. tectorum* in the untreated strips by disking in late spring. However, the disk treatment was too late to be effective.

Fall germination of the seeded grass was excellent. It soon became evident, however, that *B. tectorum* control was highly variable over the seeding. An opportunity was thus afforded to study the influence



of different levels of *B. tectorum* competition on the survival and growth of *A. spicatum* seedlings.

#### SEEDLING SURVIVAL

Ten locations were selected where 3 levels of *B. tectorum* density could be found within a 20 m radius of the center witness stake. All of these locations were on the shallow phase of the biscuit scabland complex. Attention was given in selection for uniformity of soil depth and moisture conditions.

*B. tectorum* density classes were described as sparse (0-5% canopy coverage), moderate (45-55%), and dense (95-100%) (Daubenmire 1959). Three plots, each 1 m sq, were randomly established in each density class at each of the 10 locations, making a total of 9 plots per location or an overall total of 90. Sparse plots contained from 0 to 4 *B. tectorum* plants per plot, moderate 15 to 20, and dense 90 to 100 (Figs. 2, 3).

*Agropyron spicatum* seedling counts were taken in June 1960, October 1960, and June 1962. Counts on the latter date were found to be highly inaccurate.



FIG. 2. *Agropyron spicatum* at Harder Ranch, June 1962, growing in sparse *Bromus tectorum*.

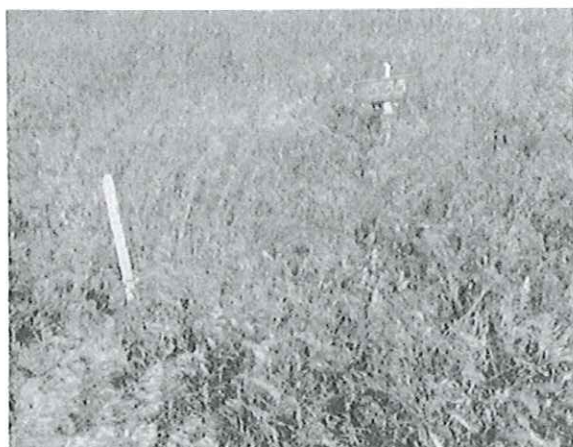


FIG. 3. Dense *Bromus tectorum* stand containing suppressed *Agropyron spicatum* plants. Harder Ranch, June 1962.

TABLE 1. *Agropyron spicatum* survival under three intensities of *Bromus tectorum* competition, Harder Ranch site, 1960.

	<i>Agropyron spicatum</i> seedlings		
	June 1960 Aver. No. per plot	October 1960 Aver. No. per plot	Average Survival (%)
Dense <i>B. tectorum</i> .....	30	11	39 <sup>a</sup>
Moderate <i>B. tectorum</i> ....	36	24	69 <sup>b</sup>
Sparse <i>B. tectorum</i> .....	36	30	86 <sup>c</sup>

Exponent letters that differ indicate significance at the .01 level of probability.

Adjacent seedlings which were counted separately in the 1960 observations frequently had merged through root crown expansion by 1962.

Seedling survival over the summer period of 1960 was inversely related to *B. tectorum* density (Table 1). Only 39% of the seedlings survived the summer in dense *B. tectorum*, while 86% survived in sparse *B. tectorum* stands. Even 39% survival is considered relatively high, when it is recalled that under natural field conditions *A. spicatum* seedlings are essentially never able to survive dense *B. tectorum* competition. Dense competition in this study averaged about 90 to 100 plants/sq m. Hull & Stewart (1948) report southern Idaho *B. tectorum* stands to vary from 300 to 1,000 plants/sq ft (approx. 0.1 sq m), or up to 100 times the density found on these plots. They observed that seeded perennial species could successfully establish in *B. tectorum* stands thinned to 50 or even up to 100 plants/sq ft. Nevertheless, the levels of *B. tectorum* density in this study effectively demonstrate the severity of increasing *B. tectorum* competition upon *A. spicatum* seedling survival.

#### MOISTURE CONTENT AND HERBAGE YIELD OF SEEDLINGS

Five composite samples of leaves and stems of 50 *A. spicatum* seedlings each were collected on July 25, 1960, from dense and five from sparse *B. tectorum* stands. The seedlings at this time of year were in the vegetative growth stage, since almost none reproduced during the first year.

Fresh and oven-dry weighings gave data relating to comparative moisture content and herbage yields. A comparison of *A. spicatum* seedling moisture content and dense and sparse *B. tectorum* sites (Table 2) provides a clue to the reason for the outcome in the survival data discussed above. *A. spicatum* seedlings growing essentially without *B. tectorum* competition averaged 43.2% moisture content. By contrast, the *A. spicatum* seedlings growing in dense *B. tectorum* averaged only 15.8% moisture. At this time the seedlings growing in sparse *B. tectorum* averaged 9.2 and 7.5 times as heavy (green weight and dry weight, respectively) as those growing under dense *B. tectorum* competition.

Similar data from June 1962 observations show that early and continued competition from *B. tectorum*



TABLE 2. *Agropyron spicatum* height, weight, and moisture content as influenced by three intensities of *Bromus tectorum* competition, Harder Ranch site.

	<i>Agropyron spicatum</i> Seedlings				<i>B. tectorum</i> Seedlings
	% Moisture July 25, 1960 %	Av. Weight (oven dry)		Av. Height June 1960 (cm.)	Av. Height June 1960 (cm.)
		July 25, 1960 (grams)	June 15, 1962 (grams)		
Dense <i>B. tectorum</i> .....	15.78 <sup>a</sup>	.076 <sup>a</sup>	1.78 <sup>c</sup>	17.5 <sup>a</sup>	58.0 <sup>c</sup>
Moderate <i>B. tectorum</i> .....				31.1 <sup>b</sup>	54.2 <sup>c</sup>
Sparse <i>B. tectorum</i> .....	43.18 <sup>b</sup>	.571 <sup>b</sup>	10.41 <sup>d</sup>	38.2 <sup>b</sup>	43.2 <sup>bc</sup>

Exponent letters which differ for comparable figures indicate significance at .01 level of probability.

suppressed the growth of surviving seedlings. *B. tectorum* distribution patterns on the study area remained essentially unchanged from 1960 to 1962. Wherever *B. tectorum* was sparse in 1960, *A. spicatum* plants controlled the site almost to the exclusion of *B. tectorum*. Where dense *B. tectorum* suppressed the *A. spicatum* seedlings in 1960, *B. tectorum* continued to dominate the site in 1962 (Fig. 4, 5). However, *A. spicatum* seedlings in the dense *B. tectorum* stands did make slow progress toward overcoming the disparity in weight evident in 1960. By the spring of 1962, seedlings grown in sparse *B. tectorum* averaged 10.41 g each, an 18-fold increase over the 1960 weight. On this date, seedlings suppressed by dense *B. tectorum* competition averaged 1.78 g, which represents a 23-fold increase over the 1960 average seedling weight.

Leaf heights of *A. spicatum* seedlings measured in July 1960, exhibit an inverse relationship, whereas

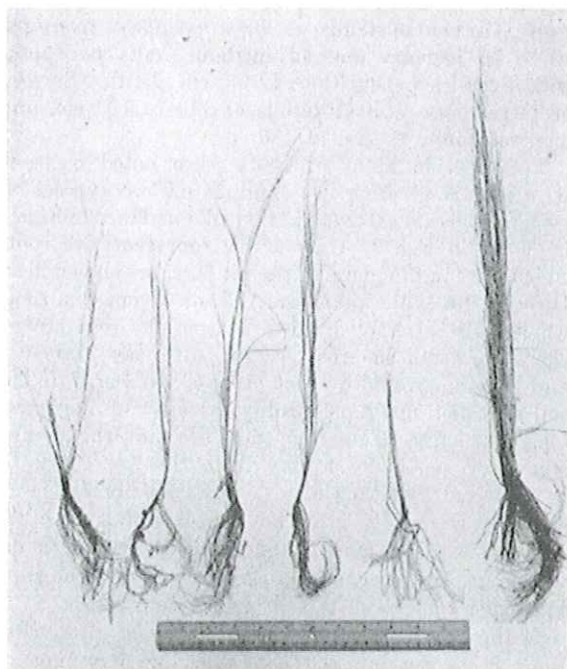


FIG. 4. Typical *Agropyron spicatum* plants collected June 1962, from dense *Bromus tectorum* site at Harder Ranch.

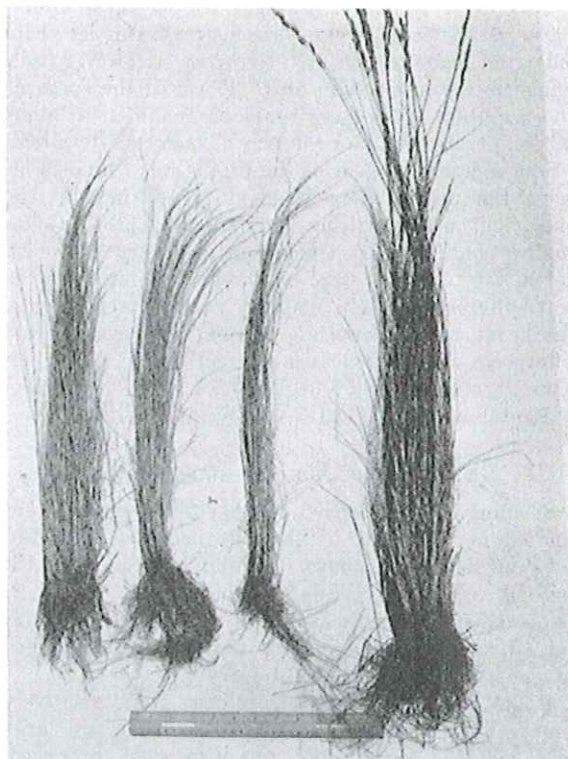


FIG. 5. Typical *Agropyron spicatum* plants collected June 1962 from sparse *Bromus tectorum* site at Harder Ranch.

*B. tectorum* heights exhibit a direct relationship, with increasing density of *B. tectorum* (Table 2). *A. spicatum* seedlings in dense *B. tectorum* competition averaged only 17.5 cm tall, less than half the 38.3 cm average height of seedlings growing under a minimum of *B. tectorum* competition. *A. spicatum* competition, on the other hand, reduced average *B. tectorum* culm heights from 58.0 cm in dense *B. tectorum*, to 43.2 cm in dense *A. spicatum*, a reduction of about 25%.

#### SOIL TEMPERATURE AND MOISTURE

Pits were excavated to a depth of 15 dm in dense and sparse *B. tectorum* stands at 3 of the 10 locations between July 25 and 28, 1960. Pits in dense and



sparse *B. tectorum* were dug simultaneously at each location. Soil temperatures were observed at 10 cm intervals in the fresh pit sides using mercury-in-glass thermometers. Observations were made between 1:00 and 3:00 p.m. Shaded air temperatures 1 m above the soil surface ranged from 38 to 40 C.

Soil samples for moisture determinations were also removed from the fresh walls of the pit. Wilting percentage determinations were made on samples collected from the same points in the pits, to allow estimates of water availability. The pressure membrane method of Richards & Ogata (1961) was followed, extracting the moisture to 15 atm pressure.

Soil temperatures range from 56 C at the surface to 23 C at 1 m depth. Surface temperatures under sparse *B. tectorum* cover were generally higher than under the shade of dense *B. tectorum*. However, this influence was lost within 10 to 20 cm of the surface. No significant differences could be found in average soil temperatures under the two *B. tectorum* densities.

Soil moisture content of the profile was found to be below the wilting percentage at the 20 and 50 cm levels, but above wilting at 100 cm depths. Color changes indicating a transition from dry to moist soil in the pit walls were observed at about 60 to 80 cm. Differences in soil moisture content were highly significant with increasing depth. However, mean differences in soil moisture content under sparse or dense *B. tectorum* were negligible, as were differences by depths under the two *B. tectorum* densities.

#### ROOT DISTRIBUTION AND MORPHOLOGY

Seedling root systems of the two species were studied in the walls of the pits excavated in July 1960 as described above. Employing the ice pick method, roots of plants in sparse and dense *B. tectorum* stands were examined to determine lateral spread, number of secondary roots, maximum depth of penetration, and habit of growth.

Roots of *A. spicatum* seedlings were relatively simple to trace from the pit wall. They are large in diameter, tough, and not profusely branched. *B. tectorum* roots were infinitely more difficult to remove, owing to their extremely weak structure and diffuse branching. A complete individual root system of *B. tectorum* has not been removed from a natural field site. Hulbert (1955) excavated and drew the main root of a *B. tectorum* plant, but he shows no secondary root development of any consequence. *B. tectorum* plants grown under similar field conditions, and excavated in the current study have all had several sizable secondary branches subdividing from the primary root (Fig. 6).

First season *A. spicatum* seedlings excavated from dense *B. tectorum* stands averaged 2 stems of 3 leaves each. In sparse *B. tectorum* stands, plants averaged 4 to 5 stems with 5 leaves each. None of the smaller *A. spicatum* plants in the dense *B. tectorum* produced seed heads, while several in the sparse stand did.

In dense *B. tectorum*, excavated *A. spicatum* seedlings averaged 6 to 7 primary and adventitious roots

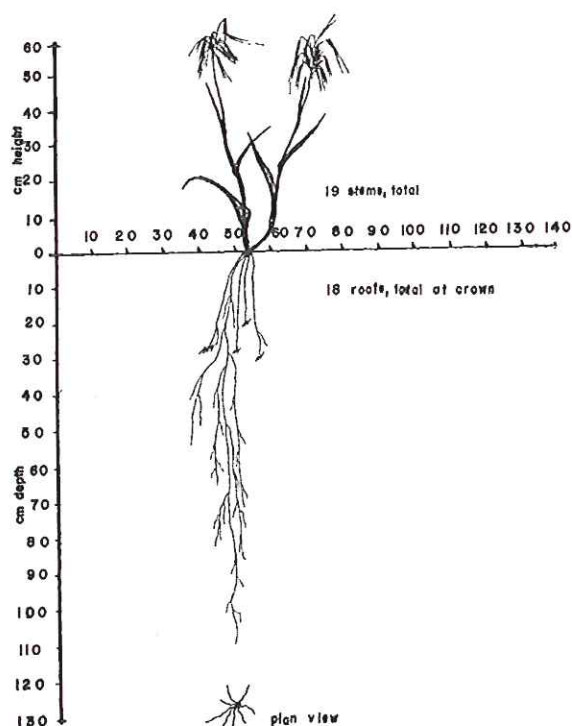


FIG. 6. Diagram of *Bromus tectorum* plant excavated at Harder Ranch site, July 1960.

per plant, which penetrated the soil to a depth of 50 to 60 cm with a few at greater depths. Survival certainly must have been dependent upon roots reaching the deep moisture supply (beyond 60 cm in this case). In sparse stands, *A. spicatum* plants averaged 12 to 15 primary and adventitious roots per plant with average penetration to 95 cm depth. Several of these roots reached depths of 110 to 120 cm, and one was found to end at 136 cm.

Two specific kinds of roots were noted on each *A. spicatum* seedling. A diagram of two typical *A. spicatum* plants excavated from pits at Harder Ranch is shown in Fig. 7. Only a few representative roots which were in the plane of the pit face, are shown here. Directly under the plant are 1, 2, or 3 very fine roots which grow directly downward from the root crown. They are small in cross section, diversely branched, and heavily covered by root hairs (X in Fig. 7). The soil does not shake off readily, because of the many long root hairs. These fine roots are the primary and secondary roots, developing from the mesocotyl. It is suspected that they may be annual, aborting later. They grow rapidly into the subsoil and sustain the seedling while a more elaborate root system is developing. However, if competition is severe, the seedling must survive on this primary root system.

If the site is sufficiently good, a system of adventitious roots develops. These may or may not accompany tillering at the lower stem nodes. Roots in this category are noticeably heavier in structure, lighter in color, less branched, and have fewer root



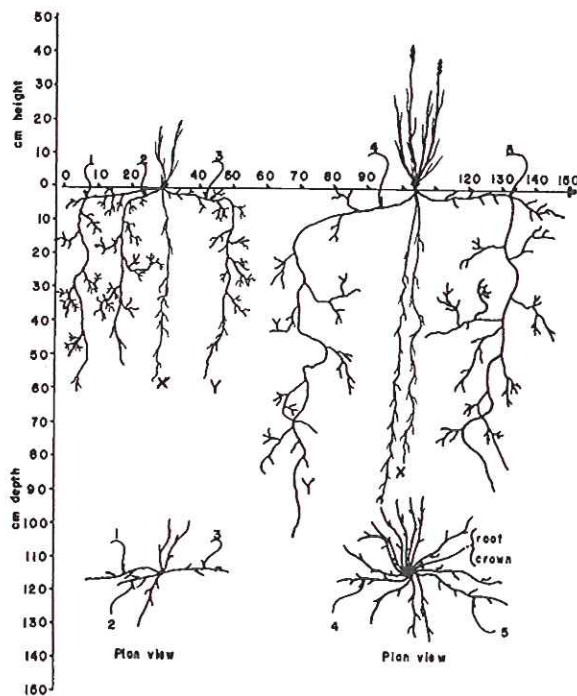


FIG. 7. Diagram of *Agropyron spicatum* root systems excavated at Harder Ranch site, July 1960. Plant on left from dense *Bromus tectorum*; plant on right from sparse *Bromus tectorum*.

hairs than the primary roots (Y in Fig. 7). They come out of the soil easily and the soil particles shake off readily, apparently because root hairs are fewer and shorter. Presumably they are larger because they arise from nodes higher on the stem. These nodes are larger as a consequence of having more vascular bundles.

Adventitious roots of *A. spicatum* seen in this study invariably grew almost parallel to the soil surface for 20 to 30 cm before turning downward. This tendency may be noted in Figs. 7 and 8. Such a habit of root growth could explain the wide spacing of *A. spicatum* plants in the field.

It is not unusual for root branches of *A. spicatum* to be unaffected by geotropism. Many root branches were observed to grow upward. One excavated root which reached 62 cm down the pit wall measured 94 cm when stretched out, an increase of 50% in length.

This general habit of root growth, wherein adventitious roots parallel the surface for some distance, has been verified in native stands of *A. spicatum* at various locations in Washington, Oregon, and Idaho. It appears that this character varies widely with location, with some ecotypes reacting similarly to the Whitmar strain used in this work, while in others roots grew almost straight down from the root crown. Perhaps this is a genetically controlled character which varies as does awn length, rhizomatousness, and leafiness in this highly plastic and widely adapted taxon.

Root characteristics of *B. tectorum* were very similar in both dense and sparse stands. A robust

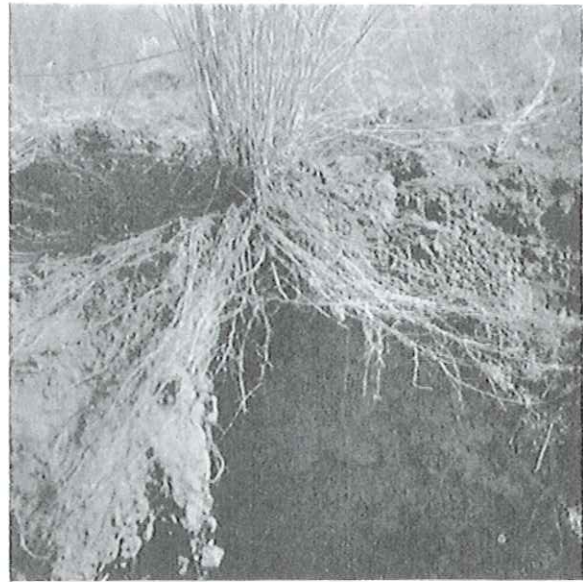


FIG. 8. *Agropyron spicatum* plant at Harder Ranch site with upper roots exposed. Note absence of roots directly under crown.

plant with 19 culms (all bearing mature inflorescences) had 8 major root trunks at the crown. Most *B. tectorum* roots appeared to terminate at about 105 cm, with a few going beyond to a maximum observed depth of 117 cm.

Primary and adventitious roots are present in *B. tectorum* seedlings also. As in *A. spicatum*, primary roots are smaller and more diffusely branched than are the adventitious roots. Tillers are commonly produced in the top and parallel development of adventitious roots occurs during the winter if growth factors are favorable (Fig. 6). Again, if competition is severe, the seedling survives on its primary root system, with no adventitious roots developing. While adventitious roots are growing, the primary system also is extended.

Both primary and adventitious roots of this species tend strongly to grow straight down. The primary system seldom branches until it reaches a depth of about 10 cm.

Roots of *B. tectorum* can readily be distinguished from those of *A. spicatum* by color and morphology. *A. spicatum* roots are off-white; *B. tectorum* roots are dark brown. *B. tectorum* roots are smaller in diameter, weaker in tensile strength, very noticeably more diversely branched, and have more and longer root hairs.

A limited sample was taken of the number of roots passing vertically through a projected 1 sq dm plot at 40 cm depth in the soil. *Agropyron spicatum* was sampled under a full stand in a sparse *B. tectorum* site. The count averaged approximately 8 roots/plot, with a range of 3 to 19. Under a dense *B. tectorum* stand, *B. tectorum* root density was too great for accurate counting, but was estimated to be in excess of 200/dm on the basis of remaining roots after excava-



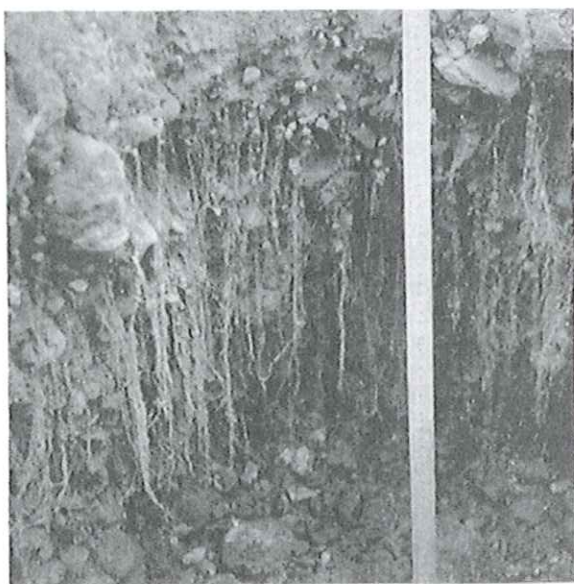


FIG. 9. *Bromus tectorum* roots exposed under a dense stand. Approximately 50% of roots lost in process of excavation.

tion (Fig. 9). Roots in Fig. 9 were extracted with great care, and yet an estimated 50% were carried away, and are not shown in the photograph. Careful field inspection revealed at least one root hair in practically every soil pore space.

#### ANATOMY

Immature leaves and mature roots were selected for microscopic study. Roots were sampled at 10, 40, and 80 cm depth, to compare root anatomy of the two species in the developmental stages at which they compete with each other. Mature roots of grasses are difficult to section owing to high silicon content of cell walls. Consequently, the number of slides suitable for examination was limited. But they represent the first known attempts to characterize the anatomy of the roots of these species.

#### LEAVES

Leaves of these two species have essentially the same anatomical structures, though they are quite different in size and shape (Fig. 10). Leaves of *A. spicatum* are narrow and obviously involuted, with somewhat heavier cell walls and thicker veins than *B. tectorum*. *B. tectorum* leaves are wider and relatively thinner. *B. tectorum* leaves are normally exposed to less moisture stress than *A. spicatum* leaves, due to differences of seasonal growth.

#### ROOTS

Anatomy of the root structure of these two species is also basically similar but differs in important detail (Fig. 11). In both species the cortex has been sloughed off, leaving the endodermis exposed at the periphery. Both have the typical vascular structure of the Monocotyledoneae with central protoxylem

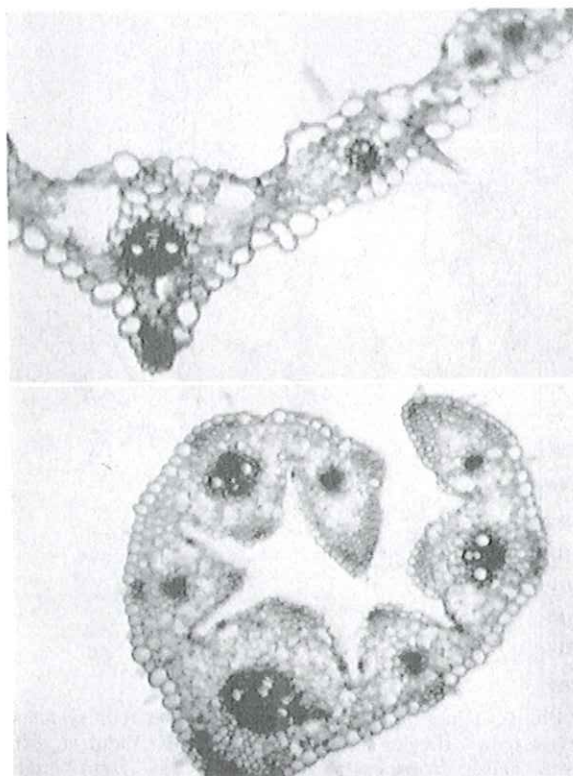


FIG. 10. Photomicrographic comparison of the leaf transections of *Bromus tectorum* (above) and *Agropyron spicatum* (below) (approximately 180 x).

tissue and scattered bundles containing metaxylem and phloem tissues. Here the similarity ends, however. In addition to being almost 100% larger in cross-sectional area, *A. spicatum* roots have tremendously heavier cell structure throughout. A critical area of cell wall thickening is in the endodermis, where it can be seen that cells in *A. spicatum* roots are heavily suberized. *B. tectorum* roots show only a fraction of the thickness found in the endodermis of *A. spicatum*. It is not difficult to visualize the difference in tensile strength previously noted for the roots of these two species, nor to understand why *B. tectorum* matures and dries out when surface soils become hot and dry in later spring.

#### GERMINATION AND GROWTH RATES

Both species produce seed regularly each year. *B. tectorum* seed matures in the late spring or early summer, falls to the ground, and germinates with fall rains. *A. spicatum* seed matures in midsummer, and shatters progressively over a period of several weeks after that date.

#### FIELD GERMINATION

*B. tectorum* germinates in the fall with the onset of cool, wet weather and short days. Hulbert (1955) reported that newly ripened seed germinated very poorly at high temperatures or in light. However, after 3 months of after-ripening these factors exerted



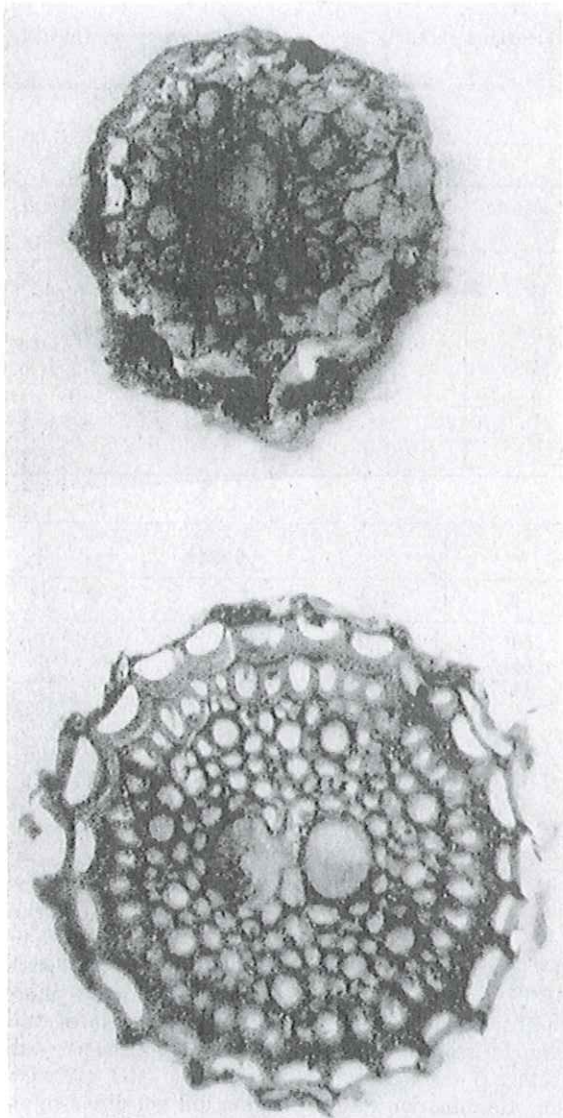


FIG. 11. Photomicrographic comparison of root transverse sections of *Bromus tectorum* (above) and *Agropyron spicatum* (below) (approximately 350 x).

less influence. In the field, the onset of fall weather brings reduced soil temperatures and light intensities. "Thus the internal changes in response are correlated with seasonal changes in environment . . ." and germination occurs in the fall (Hulbert 1955).

If summer is unusually cool and wet *B. tectorum* will germinate. In mid-August 1961, a period of cool, wet weather occurred in eastern Washington. An estimated 15% of the *B. tectorum* seed germinated on 10 selected 1 m sq plots. Within 2 days, hot, dry weather returned and all of these seedlings died.

Records of germination of *A. spicatum* under natural conditions are rare. To make a record of such germination, a study was initiated in the Palouse Natural Area, located about 20 mi south of Pullman, Washington. The site was classified as an *Agropyron*/

*Poa* habitat type (topographic climax), with climate very similar to that described for the Pullman Nursery site. Seed of *A. spicatum* and *B. tectorum* was collected for the experiment in August 1962 from the experimental area. On September 5, 1962, 3 small plot locations were established, before seasonal rains began. A plot consisted of a bare area 15 by 30 cm between large established *A. spicatum* plants. The surface 5 mm of soil was removed along with litter and extraneous seeds found there. One hundred seeds of *A. spicatum* and *B. tectorum* were scattered in separate spots at each of the 3 plots. These were then covered uniformly with approximately 3 mm of fine soil.

Observation on September 18, 1962, following 28 mm of precipitation which fell September 10 through 13, showed 16% germination of *A. spicatum*, and 17% germination of the *B. tectorum* seed. Natural seed of annual plants native to the area (both grasses and broad-leaved species) were noted to be germinating on this date also. Subsequent observations, continuing until December 21, 1962, failed to disclose any further germination of either species. Laboratory germination tests at 20 C over a 5-day period resulted as 53% and 84% germination, respectively, for *A. spicatum* and *B. tectorum* seed used in the trials.

#### TEMPERATURE AND WATER POTENTIAL

A factorial experiment was designed to test the influence of various temperatures (10, 20, 30 C) and water potentials (0, 5, and 10 atm) on germination of the study species. Seeds were exposed to germinating conditions by placing them in 15 cm diameter petri dishes on a 2% agar-agar substrate.

Water potential was controlled by mixing d-mannitol at various concentrations in the agar-agar substrate. Desired tensions were calculated as follows (Knipe & Herbel 1960):

$$g = \frac{PV_m}{RT}$$

where  $g$  is grams of mannitol required,  $P$  is desired water potential,  $V$  is volume in liters,  $m$  is molecular weight of mannitol (182),  $R$  is .08205 liter atm/degree mole, and  $T$  is absolute temperature. Stock solutions were mixed by adding 40 g of agar-agar to 200 ml of distilled water. To arrive at 5 atm water potential, 75.8 g of mannitol were added to the stock solution, and 151.6 g for 10 atm. None was added for the 0 atm water potential mixture. These concentrations were later verified by use of a Peltier psychrometer and found actually to be 6.2 and 11.4 atm rather than 5 and 10 as calculated.

Temperatures were maintained in three separate, darkened, constant-temperature germination chambers. All treatments were run concurrently. Previous tests had demonstrated that continuous darkness (except during examination for counting germinated seeds) did not inhibit germination. Temperatures of 10, 20, and 30  $\pm$  1 C were maintained throughout the germinating period.

Petri dishes, each containing agar-agar at a specified



TABLE 3. Influence of temperature and water potential variations on early germination of *Agropyron spicatum* and *Bromus tectorum*.

Water Potential (atmospheres)	Temperature (C)	Germination			
		4 days		6 days	
		A. spicatum (%)	B. tectorum (%)	A. spicatum (%)	B. tectorum (%)
0.....	10	0	1	2	23
	20	33	36	66	51
	30	31	26	50	33
6.2.....	10	0	0	0	12
	20	14	20	44	37
	30	16	11	30	14
11.4.....	10	0	0	0	0
	20	1	4	14	11
	30	0	3	2	6

Analysis of variance, percent germination

Source	4 days			6 days		
	D.F.	M.S.	F.	D.F.	M.S.	F.
Temperature.....	2	1625	50**	2	4269	82.6**
Water potential.....	2	1788	55**	2	4604	88.5**
T x W.P.....	4	442	14**	4	482	9.3**
Error "A".....	18	32		18	52	
Species.....	1	3	.2	1	96	5.1*
S. x T.....	2	45	3.5*	2	623	33.5*
S. x W.P.....	2	5	.4	2	28	1.5
S. x T. x W.P.....	4	14	1.1	4	196	10.5**
Error "B".....	18	13		18	18.6	
Total.....	53			53		

\*Significant beyond the 5% level of probability.

\*\*Significant beyond the 1% level of probability.

water potential were subdivided into halves by scalpel streaks on the surface. One hundred seeds of each of the two species were placed in each dish. Three replications at each of the 3 water potentials were placed in each constant temperature box. Thus there were 9 petri dishes in each of 3 temperature boxes, with each dish containing 2 species, for a total of 54 sample units. Observations of germination were made daily at a given hour. Germination was defined as the appearance of a minimum radicle 2 mm in length. Data for the fourth and sixth days are summarized in Table 3. These results show initial response, which is of greatest significance to competition.

At the end of 4 days, overall germination averaged 11%. Both temperature and water potential variations resulted in significant changes in germination. Considering the 2 species together, germination averaged 21.2, 8.5 and 1.3%, respectively, at 0, 6.2, and 11.4 atm water potential. There was no overall difference in germination of the 2 species at the end of 4 days.

In 4 days at 10 C there was practically no germination in either species. Incipient germination was indicated in *B. tectorum* at 0 potential on this date, but none at the higher water potentials. Germination of *B. tectorum* was higher at 20 C than 30 C (20 vs.

13% germination, respectively), verifying Hulbert's (1955) conclusion that this species germinates more readily at moderate temperatures. He relates this characteristic to the necessity for cool, moist fall weather if the seedlings are to survive after germination. Germination of *A. spicatum* did not differ significantly at the two higher temperatures.

At the end of 4 days, the 2 species had reacted quite similarly to changes in temperature as water potential was varied (second order interaction).

Germination overall increased from 11% at 4 days to 22% at 6 days. Temperature and water potential continued to cause significant differences in response. Considering the 2 species together at 6 days, germination was 6, 37, and 22%, respectively, at 10, 20, and 30 C, and 37, 22, and 6%, respectively, for 0, 6.2, and 11.4 atm water potential. The tendency for higher germination at 20 C than at either 10 or 30 C continued as at 4 days germination time.

*Agropyron spicatum* germinated less than 1% at 10 C, while 6% of the *B. tectorum* germinated at this temperature. Both species germinated better at 20 C than at 30 C, with *A. spicatum* showing slightly higher (21 and 14%, respectively) values than *B. tectorum* (16 and 9%, respectively). Germination of the 2 species did not react differently to increasing water potential.



The 2 species reacted differently to changes in temperature and water potential (second order interaction). This results from the higher germination rate for *B. tectorum* at low temperature associated with low water potential, as well as at high temperature associated with high water potential.

#### SEASONAL GROWTH WITHOUT COMPETITION

After fall germination, both species appear to lie dormant during the coldest winter months, and resume growth in the spring. A detailed field study of the rates of root and leaf elongation were made at the Pullman Nursery in the winter of 1963-1964.

A battery of 20 glass tubes, 51 mm in diameter and 1.2 m long, were arranged in orchard auger holes at 17° from the vertical plane, so the roots would grow against the glass for observation. These were arranged so the tops of the tubes were slightly above, and the soil surface in the tubes even with, the general soil surface of the land. They could be lifted out for observation at will. Tubes were in full length contact with the soil profile; preliminary tests demonstrated a close correlation between soil temperatures in the tubes and in the adjacent profile at all depths. The tubes were divided into 2 groups of 10, each group being seeded to 1 of the 2 species being studied. Measurements were made of maximum root depths and leaf heights at approximately weekly intervals over a 10-month period, October to July. In addition, numbers of primary and adventitious roots, numbers of leaves, and numbers of stems were counted at frequent intervals. Presence of snow made leaf and stem counting very difficult so these observations were discontinued during the snow period.

Within the same experimental area described above, soil temperature data were collected for depths of 10, 25, 50, 75, and 100 cm. This activity was begun on December 13, 1963 and continued into July, 1964. Mercury-in-glass thermometers were left in contact with the soil in the bottoms of separate holes of appropriate depths. The bulbs were covered with sealing wax to slow temperature changes when the ther-

mometers were brought up for observation. The openings to the test holes were closed with rubber stoppers through which the retrieving cords passed. Two identical sets of thermometers provided replicated readings.

#### RATE OF ROOT GROWTH

Seed of both species were pregerminated before being placed in the field on October 4, 1963. Roots of *B. tectorum* were readily visible, following the lower side of the tube. The initial roots of *A. spicatum*, however, grew to the upper side of the tube in most instances, before appearing on the lower side. Root growth was not evident on the lower side in all tubes until the November 22 observation (Table 4).

*Agropyron spicatum* roots grew rather slowly from the October 11 observation until mid-November, when growth ceased almost entirely (Fig. 12). Soil temperatures at the average *A. spicatum* root tip depth was 0°C on December 13 and remained at near freezing temperatures until late March 1964. During this 3-month period, the average maximum root length of this species increased only about 5 cm. On May 19, *A. spicatum* roots were short and stocky. Adventitious roots were relatively abundant, but averaged only 200 mm in length.

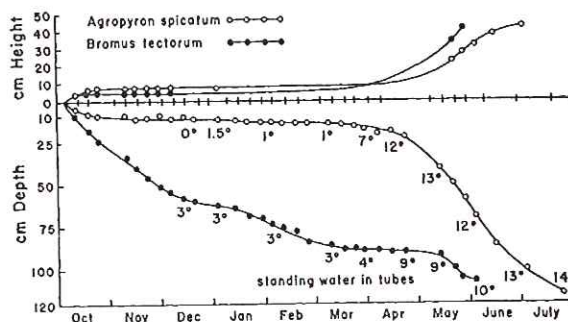


FIG. 12. Seasonal leaf and root growth of *Agropyron spicatum* and *Bromus tectorum* in glass tubes in the field (1963-1964). Leaf heights represent tallest leaf, and root depths represent longest visible primary root tip.

TABLE 4. Number of leaves, stems, and main roots, by dates, on plants grown in glass tubes, 1963-1964.

	Leaves (Average Number)		Stems (Average Number)		Main Roots (Average Number)	
	<i>A. spicatum</i>	<i>B. tectorum</i>	<i>A. spicatum</i>	<i>B. tectorum</i>	<i>A. spicatum</i>	<i>B. tectorum</i>
Oct. 11.....	1.0	1.0	1.0	1.0	0.2	0.8
Oct. 18.....	1.9	1.8	1.0	1.0	0.5	0.8
Oct. 25.....	2.6	2.7	1.0	1.1	0.6	1.1
Nov. 8.....	2.7	4.8	1.0	1.1	0.8	2.8
Nov. 15.....	2.9	6.9	1.0	2.4	0.8	3.2
Nov. 22.....	3.0	7.7	1.0	2.9	1.1	3.5
Nov. 29.....	3.1	8.9	1.0	3.1	1.2	3.7
Dec. 6.....	3.4	8.9	1.0	3.1	1.3	3.7
Jan. 3.....	3.1	10.3	1.2	3.1	1.4	3.9
Feb. 9.....					1.7	4.0
May 19.....	12.6	32.9	3.2	6.6	6.6	15.6
June 12.....	21.5		6.4		12.6	
July 1.....	37.7		9.0		23.4	



With the coming of spring and increasing temperatures, the rate of *A. spicatum* growth increased rapidly. Between March 29 and July 22, the average root length increased from about 170 mm average length to in excess of 1150 mm. Spring and early summer are the times for root growth in this species. Rapid root growth coincides with rapid leaf growth in *A. spicatum*.

*B. tectorum* roots begin growth at a more rapid rate than *A. spicatum* (Fig. 12) and continue growth all winter. Soil temperatures average from 2 to 3 degrees warmer at the root tips of *B. tectorum* than at shallower depths where *A. spicatum* root tips were found. This may be a critical difference where chemical changes relating to cell division at root tips must precede growth.

The root growth curve of *B. tectorum* leveled off in late March, showing little additional growth in April and early May. During this period surface water from snowmelt and spring precipitation entered the holes, filling them approximately to the level of the *B. tectorum* root tips. This could explain the spring cessation of growth in *B. tectorum* roots noted above. Or, it might be explained by diversion of photosynthate to increased growth of either adventitious roots or tillers. However, the water level explanation seems most acceptable. Contrasted to *A. spicatum*, primary *B. tectorum* roots grow mainly during the winter when leaf growth is much reduced. Adventitious roots in *B. tectorum* grew rapidly during the winter also. On January 2, five *B. tectorum* plants had adventitious roots averaging 499.8 mm in addition to much longer primary roots. Numerous other adventitious roots were also observed on each of these five *B. tectorum* plants.

The average number (primary plus adventitious trunks) of main roots increased continuously throughout the winter in both species (Table 4). Between time of germination and November 15, *A. spicatum* roots were more or less unavailable for observation as previously noted. Of 10 plants observed in October 4, only 2 had roots visible on the face of the tube. The number increased steadily through 5, 6, and 8 until on November 22, 9 plants each exhibited 1 root, while 1 plant had 2. Adventitious roots of *A. spicatum* continued to increase slowly through the winter, until on May 19 the average number was 6.6. Two months later the average number had increased to 24.5 roots.

Average number of *B. tectorum* roots increased more rapidly than in *A. spicatum*. By November 15 the average *B. tectorum* plant had 3.2 roots. This number increased very slowly through the winter into February. The only spring count, on May 19, indicated that an average plant had 15.6 roots at that time. Soon after the May 19 date, rodents grazed all the *B. tectorum* stems and rendered further records valueless.

#### LEAF AND STEM GROWTH

Leaves of *A. spicatum* averaged approximately 10 mm taller than *B. tectorum* leaves throughout the

winter (Fig. 12). However, with the advent of warm spring weather, *B. tectorum* leaves and reproductive stems elongated rapidly, temporarily surpassing *A. spicatum* in stature. The period of maximum *A. spicatum* leaf elongation was approximately the same as its period of maximum root growth. On the other hand, the period of maximum leaf elongation in *B. tectorum* occurred in mid-spring, following the winter period of maximum root elongation. Average leaf height data indicate that averages decreased slightly at times during the early winter. This was due to attrition in handling, grazing by rodents, and other forms of destruction during the period of very slow winter growth.

The volume of leaf growth produced through the winter is more accurately indicated by the number of leaves and stems than by leaf height data. Counts shown in Table 4 disclose a winter plateau in the average number of leaves and stems per plant of *A. spicatum*, followed by a spring burst in growth. *B. tectorum* produced more of both leaves and stems throughout the winter, and arrived at a peak of activity approximately 6 weeks earlier than *A. spicatum*.

*Bromus tectorum* was in early flower stage of development at the May 19 observation. Every plant produced flower stalks. *A. spicatum* seedlings remained in vegetative condition until July 1, when 1 plant was found in early boot stage. All plants were destroyed by rodent grazing before flowering was completed.

Though *A. spicatum* seedlings appeared to be much less vigorous than *B. tectorum* seedlings in fall and winter, in the culmination of its first season of growth (without competition) it produced more leaves, stems, and main roots and grew to a greater total leaf height than did *B. tectorum* at its peak.

#### SOIL MOISTURE RELATIONSHIPS

It should now be clearly evident that *B. tectorum* roots grow more rapidly in the early stages than do *A. spicatum* roots. It is not clear at this point, however, but only suspected, that *B. tectorum* roots actually exhaust the available moisture supply in advance of the competing *A. spicatum* roots, thus reducing their rate of elongation and finally causing their demise.

Solution of this puzzle required a method of accurately determining the presence of available soil moisture without unduly disturbing competing root systems. Furthermore, intertwined root systems of the 2 species had to be identified while remaining in the soil, so their position relative to available soil moisture could be established. The problem was brought into the laboratory where growth factors were more fully controllable, and sophisticated equipment could be brought to bear.

A modification of the gamma ray attenuation technique as described by Gardner (1963) was employed to determine soil moisture levels. In principle, a beam of gamma rays was projected through the ex-



perimental soil column at specified depths. A scaler, activated by a scintillation detector placed on the opposite site of the soil column from the beam source, measured its intensity. The intensity of the beam is attenuated (or reduced) by passing through the soil column. If the density of the soil (minus soil moisture) is constant, then changes in beam intensity over time can be related to changes in water content.

Root identification in the soil was accomplished through the use of  $P^{32}$ , a radioactive isotope of phosphorus. Briefly, the isotope was introduced into the vascular system of the *A. spicatum* seedlings through the leaves. It moved rapidly into the root system through natural channels. Radio-autographs were made of the *A. spicatum* root systems by placing X-ray film in contact with the side of the experimental soil column. In the same boxes, *B. tectorum* seedlings were then activated and radio-autographs made to show the combined *A. spicatum* and *B. tectorum* root systems. *B. tectorum* root systems could be recognized in the second radio-autograph by subtracting *A. spicatum* roots seen in the first radio-autograph.

No influence on plant growth could be noted as a result of gamma ray exposure in moisture determinations. Only a very small part of the boxes was exposed in the path of the 1.27 cm diameter beam, passed through at 9 depths.

#### ROOT STUDY BOXES

Plants were grown in boxes 13 cm wide, 22 cm long, and 100 cm deep. The sides were mounted for easy removal to allow visual inspection of roots and preparation of radio-autographs. They were also provided with ports which could be opened for gamma ray soil moisture determinations. Boxes were lined with .0127 mm thickness milar film to reduce moisture loss at the column sides, and to prevent loss of soil from portholes.

The soil was prepared by artificially aggregating Palouse silt loam "A" horizon material. It was first sterilized in an autoclave, after which it was thoroughly air dried. It was then completely mixed by hand shovel on a concrete floor. Kryllium (VAMA) at the rate of 0.1% by weight was added to the dry soil in a cement mixer. Aggregates were formed by adding water in a fine spray as the soil turned in the mixer. After the aggregates had air dried again, they were screened through a 2 mm sieve to remove the larger aggregates.

Mechanical analysis by the Bouyoucos (1928) hydrometer method verified the silt loam classification of the soil used. Textural composition was found to be 16% sand, 62% silt, and 22% clay.

The soil was placed in the boxes with great care to assure as uniform bulk density throughout as possible.

Distilled water was added at the top of each box over a 2-day period until visual inspection indicated that the soil at the bottom was thoroughly wetted. The boxes then stood for a period of 2 months to

TABLE 5. Arrangement of species in root study boxes.

Box Number	Species	Number of Plants	Ratio
1, 2, 21, 22.....	<i>A. spicatum</i>	224	4
	<i>B. tectorum</i>	49	1
3, 4, 23, 24.....	<i>A. spicatum</i>	49	1
	<i>B. tectorum</i>	224	4
5, 6, 25, 26.....	<i>A. spicatum</i>	136	1
	<i>B. tectorum</i>	136	1
7, 8, 27, 28.....	<i>A. spicatum</i>	273	
9, 10, 29, 30.....	<i>B. tectorum</i>	273	
11, 31.....	None	None	

drain excess water and to allow settling. No further water was added during the experiment, except as noted at planting. At the end of the waiting period, excess soil was removed to establish a permanent soil surface level 2 cm below the box tops.

Pregerminated seeds of the subject species were planted on 1 cm centers. Species combinations were arranged as shown in Table 5, using a geometric pattern which resulted in the sparse species (49 plants/box) being completely surrounded by the dense species (224 plants/box). Where equal numbers of each were planted, the species were alternated.

#### CONTROLLED GROWTH FACTORS

In the first run, January 15 to March 11, 1964, the boxes were held at  $21 \pm 2$  C night temperature and  $27 \pm 2$  C daytime temperatures in an air conditioned laboratory. Light intensity was approximately 1,000 ft-c measured at leaf level. Day length was 12 hr. Lights provided the excess heat energy which raised the daytime temperature. The first run included boxes 1 to 11, and the second run 21 to 31.

Some innovations were added in the second run. The boxes were held for most of the period in a refrigerated growth chamber, where it was possible to simulate fall field conditions of cool air temperatures and an inverted soil temperature gradient. Boxes were also tilted slightly to bring more roots to the soil surface for radio-autography. At the beginning, from July 15 to July 21, and again at the end of the run from November 3 to December 3, 1964, growing conditions were the same as described above in the laboratory. The air temperature control on the growth chamber was set a 8 C which was the lowest possible during the summer months. The boxes were sealed into an insulated jacket inside the growth chamber, with only the tops exposed. An electric heating cable was placed under the boxes and adjusted to provide 5 C higher soil temperature in the bottoms than the air temperature above. Recording thermometers monitored air temperature, and soil temperatures at 7.5, 45, and 90 cm depth. Air temperature in the growth chamber was maintained at  $8 \pm 1$  C. Soil temperatures at 7.5 cm varied from day to night, reaching a high of 10 C at 6 PM and a low of 8 C at 6 AM. Increased surface temperatures were the result of energy added by lights. The deeper



soil temperatures did not vary diurnally; at 45 cm the average temperature held at  $8 \pm 1$  C and at 90 cm it averaged  $13 \pm 1$  C.

#### SOIL MOISTURE DETERMINATION

Soil moisture determinations were made on 7 dates in the first run, including calibrations immediately before and after. Due to the fact that the boxes were sealed in the insulated jacket in the second run, as well as the imminent possibility of damaging the plants while transporting them .5 mi from the chamber to the laboratory, soil moisture determinations were made only at the beginning and end.

Moisture determinations were made at 10 cm intervals beginning at the 5 cm level and proceeding to 85 cm. An elevator having counterweights and preset stops was used to position the boxes in the gamma beam.

Availability of soil moisture was studied by employing the pressure membrane technique (Richards & Ogata 1961). A desorption curve was constructed to express the relationships found for the Palouse silt loam used in the growth boxes, assuming 15 atm to represent the wilting point.

At 15 atm the average soil moisture content was 11.78%. Field capacity was estimated to be approximately 22%, based on samples from the saturated root growth study boxes. Approximately half of the available moisture for this soil lies between 11.78% (15 atm tension) and 16.32% (1 atm tension). These levels are used as bench marks in the interpretation of soil moisture data.

#### ROOT IDENTIFICATION

Radioactive phosphorus was introduced into the plants by submerging clipped leaf ends in a solution containing the isotope. Five plants of each species were treated. Only those roots near the surface of the exposed soil column activated the film. Plants near the edge of the box which were most likely to have roots on the surface were chosen for treatment. Each plant received 10  $\mu$ c of radioactivity. At this level of activity satisfactory exposures could be made in 6 to 8 hr.

Three sheets of 25 by 33 cm no-screen medical X-ray film were taped end to end so as to cover the entire side of the soil column, from top to bottom. The soil boxes were tipped flat on the floor with the treated side up. In complete darkness the X-ray film was placed against the soil column, separated from it only by the milar film. A sheet of plywood was placed over the X-ray film with a thin sheet of polyfoam between for cushioning. Lead bricks were piled on top of the plywood to insure firm contact.

#### SEEDLING GROWTH

The root growth boxes demonstrated that *B. tectorum* does, in fact, exhaust soil moisture ahead of the growing *A. spicatum* roots. (Fig. 13 through 17). Plant roots remove soil moisture progressively

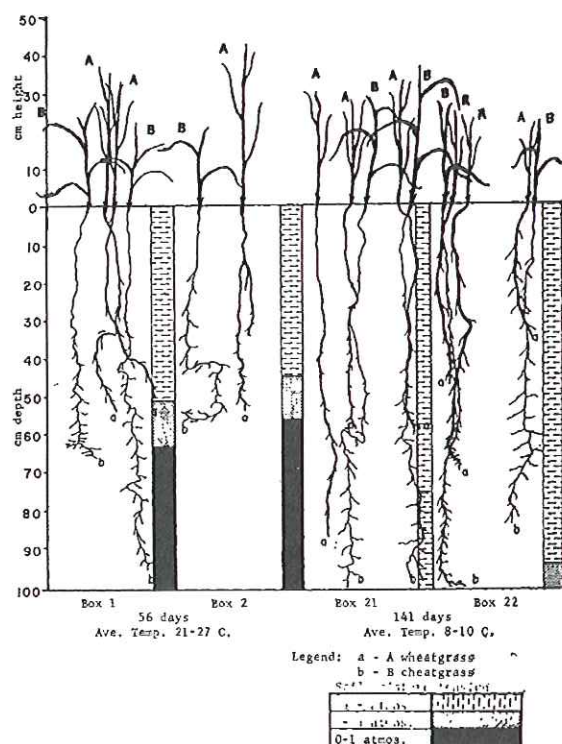


FIG. 13. Development of *Agropyron spicatum* and *Bromus tectorum* seedlings in relation to available soil moisture. Two replications of each run in high density *A. spicatum*.

from the top downward. Data in Table 6 show that for the first 2 or 3 weeks after establishment, moisture levels remained almost at field capacity, even in the surface layer. In the January 30 observation a few centimeters of soil at the top of the boxes were below 15 atm tension. At each successive observation the level of available water receded. That transpiration was removing most of the moisture can be shown by a comparison of these data with moisture data for boxes without plants. At the end of both the first and second runs, soil moisture tension did not fall below 1 atm at any point sampled in box 11 or 31, which were exposed to identical conditions with the other boxes, except that they lacked plant growth.

*Bromus tectorum* competition definitely reduced the elongation rates of *A. spicatum* seedling roots in this study. There are not enough plants showing on the radio-autographs to justify a statistical analysis, but nevertheless the indicated trends are in keeping with expected results (Table 7). The average *A. spicatum* length in boxes 9, 10, 29, and 31 (lacking *B. tectorum* competition) was 64.4 cm. The presence of 1 *B. tectorum* plant to 4 *A. spicatum* plants reduced *A. spicatum* root lengths approximately 12% (boxes 1, 2, 21, and 22). When the ratio was increased to equal numbers of each species, *A. spicatum* root growth was reduced an additional 15% (boxes 5, 6, 25, and 26), or to approximately 73% of no *B. tectorum* competition. At the highest



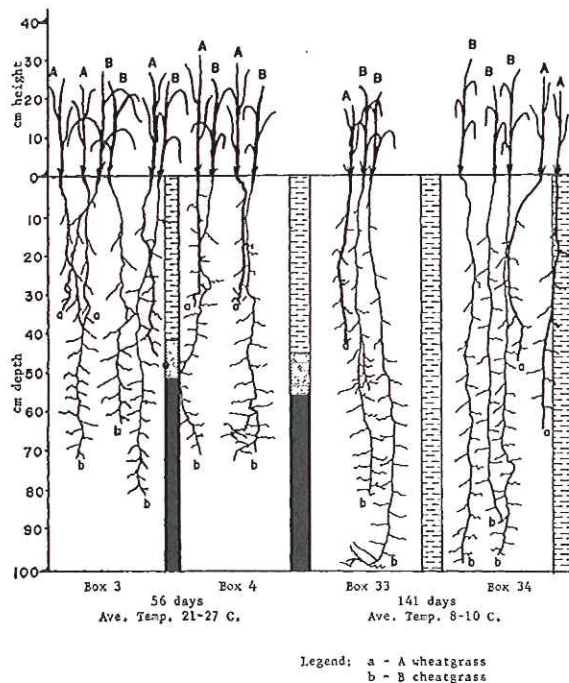


FIG. 14. Development of *Agropyron spicatum* and *Bromus tectorum* seedlings in relation to available soil moisture. Two replications of each run in high density *B. tectorum*.

competition rate, 4 *B. tectorum* plants per *A. spicatum* plant, *A. spicatum* root growth was reduced to 65%. There also appears to be a rough negative correlation between density of *B. tectorum* and number of *A. spicatum* seedlings found on the radio-autographs.

*Bromus tectorum* seedling root elongation does not appear to be influenced by *A. spicatum* seedling competition within the range of densities tested. The shortest roots were found where the least density of *A. spicatum* was present (Table 7). This seems to imply that intraspecific competition is more keenly felt by this species than interspecific competition.

Of greater significance than relative root length is the location of roots in relation to available moisture. In boxes without *B. tectorum* competition (Fig. 16), 3 of 8 visible *A. spicatum* plants have roots extending into soil with water available at less than one atmosphere tension. *A. spicatum* roots are not in this relatively low tension soil moisture zone in any box containing *B. tectorum* plants. Only the tips of a few *A. spicatum* roots growing in competition with *B. tectorum* reach into the zone of moisture available between one and 15 atm tension. Thus most of the *A. spicatum* roots are found in soil with moisture tension above 15 atm. On the other hand, in the boxes of the first run, *B. tectorum* roots extend well down into the zone of soil moisture at tensions less than 15, or even 1 atm tension. Up to 50% of the

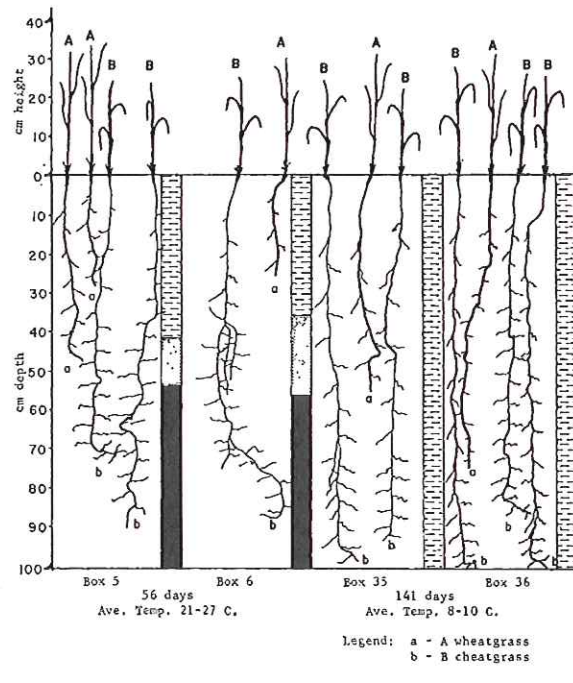


FIG. 15. Development of *Agropyron spicatum* and *Bromus tectorum* seedlings in relation to available soil moisture. Two replications of each run with equal densities of each species.

total length of some *B. tectorum* roots are in soil containing moisture available at tensions less than 15 atm.

Results of the first run clearly show the relative location of the plant roots to the moisture supply. Moisture data for the second run are not so useful because the moisture level was allowed to become depleted too far before the moisture samples were taken. However, the second run root diagrams are included here as additional evidence of relative rate of root growth in support of the first run.

Plants of both species grew deeper in the second run than in the first. This is attributed to the longer growth period and to reduced transpiration stress due to the lower temperatures. The lower temperatures did not, however, appear to change materially the growth ratio between the two species.

It was the objective of the second run to simulate field conditions more nearly than in the first run. In the field, cold temperatures gave an additional advantage to *B. tectorum* root growth, as previously discussed. The capacity of the growth chamber would not allow reducing soil and atmosphere temperatures to 0 C. It is apparent both from the growth chamber data of the second run, and from soil-plant observations in the glass tube study, that *A. spicatum* seedling roots grow well at 8-10 C., but are inhibited by temperatures as low as 3 C. Thus, in a sense,



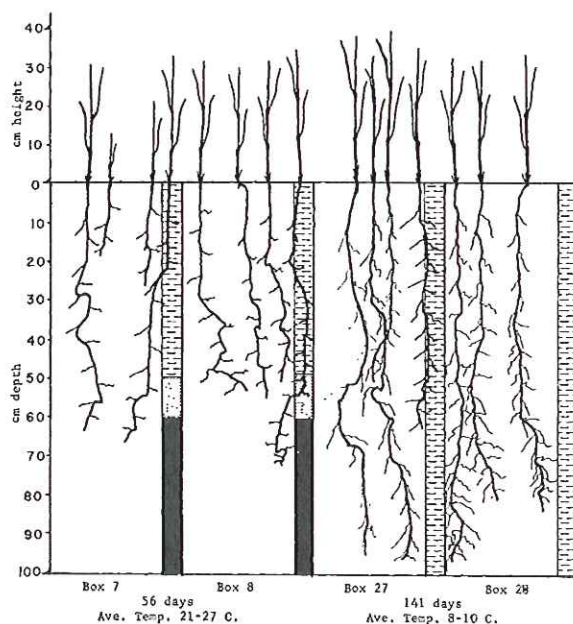


FIG. 16. Development of *Agropyron spicatum* seedlings in relation to available soil moisture. Two replications of each run in a monospecific stand.

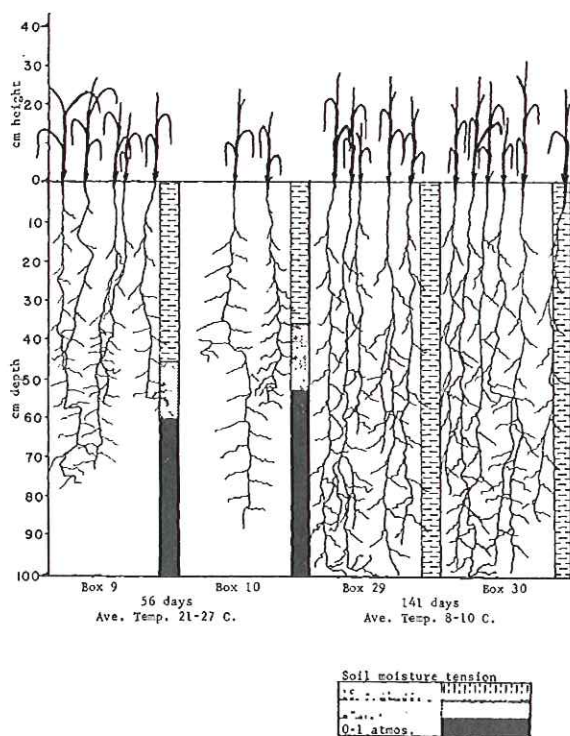


FIG. 17. Development of *Bromus tectorum* seedlings in relation to available soil moisture. Two replications of each run in a monospecific stand.

TABLE 6. Depth in root study boxes to moisture at 15 atm tension by dates, 1964. First run.

Box	Jan. 30 (cm)	Feb. 13 (cm)	Feb. 27 (cm)	March 11 (cm)
1.....	2	13	35	51
2.....	1	13	33	45
3.....	4	12	35	52
4.....	3	10	23	57
5.....	1	11	27	54
6.....	1	12	27	56
7.....	1	14	28	60
8.....	1	13	39	60
9.....	3	15	25	60
10.....	2	13	25	53
11.....	0	0	0	4

the attempt in the second run to study more closely the phenomena found in the field with the glass tube study failed. But it emphasized the changes which occur in growth rate correlated with small changes in temperature near freezing.

## DISCUSSION

Specific research results have been discussed throughout the foregoing methods and results section. Therefore the discussion here will consider these experiments as they contribute to an understanding of the overall competitive relationships between *A. spicatum* and *B. tectorum*.

*Bromus tectorum* definitely does compete strongly with seedlings of *A. spicatum*. McKell, Robinson & Major (1962) imply that *B. tectorum* stands present a "biological near-vacuum" to invading species. Further, they cite Stewart & Hull (1949) as supporting their thesis that "communities of annual plants are extraordinarily open." On the contrary, the latter authors (p. 62) say that *B. tectorum* has "great competition power." Robertson & Pearse (1945) classify *B. tectorum* stands as "closed communities" as far as range seeding is concerned. This latter view is in accord with the experience of the author, and with the experimental results reported.

However, *B. tectorum* stands may be invaded by other species under conditions not revealed in these experiments. The fact that *B. tectorum* succumbs to competition by certain other weedy species such as *Taeniatherum asperum* (Simonkai) Nevski does not mean that *B. tectorum* is a poor competitor to the seedlings of desirable, late maturing, perennial grasses.

At moderately low temperatures and in moderately moist soil, as frequently found in the fall on field sites, *B. tectorum* has a small advantage over *A. spicatum* in rate of germination. At this season of the year early germination may be important in competition because the earliest plants to germinate have the greatest opportunity for growth and establishment before inhibiting winter temperatures occur. Field observations of germination indicate that the slight advantage of promptitude of germination in *B.*



TABLE 7. Maximum root lengths in root growth study boxes (see Fig. 13 through 17).

Boxes 7, 8, 27, 28		Boxes 1, 2, 21, 22		Boxes 5, 6, 25, 26		Boxes 3, 4, 23, 24		Boxes 9, 10, 29, 30
<i>A. spicatum</i> 273 (cm)		<i>B. tectorum</i> 49 (cm)	<i>A. spicatum</i> 224 (cm)	<i>B. tectorum</i> 136 (cm)	<i>A. spicatum</i> 136 (cm)	<i>B. tectorum</i> 224 (cm)	<i>A. spicatum</i> 49 (cm)	<i>B. tectorum</i> 273 (cm)
18		67	51	75	29	63	35	55
26		96	54	90	48	72	37	57
64		57	55	88	27	81	46	72
67		97	58	91	57	71	32	77
50		100	87	99	75	72	32	58
53		81	35	86		81	42	88
55		100	47	100		100	47	62
70			68	100		87	64	67
50						96		91
62						98		100
96								100
97								100
79								78
82								87
97								91
								96
								97
Average	64.4	85.4	56.9	91.1	47.2	82.1	41.0	100 82.8

*tectorum* is not a major consideration in competition between these two species.

On the other hand, the relative abundance of seeds is important. No count of *B. tectorum* seed was made in this study, but Hulbert (1955) reports counts of 200 to 600 seeds/dm on plots at Lewiston, Idaho. The usual rate of artificially seeding *A. spicatum* in current renovation practices (8 lb/acre) provides fewer than 3 seeds/dm. Remnant plants in deteriorated *A. spicatum* stands would not produce nearly as many seeds as a vigorous stand of *B. tectorum*.

Once seeds of these 2 species have germinated, *B. tectorum* has a distinct advantage in rate of root elongation. At normal room temperatures its roots grow about 50% faster than *A. spicatum* roots. In the field, where soil temperatures are at or near freezing for long periods during the winter, *B. tectorum* has an even greater advantage. *B. tectorum* roots, which grow at greater depths due to their more rapid elongation immediately after germination, have the advantage of higher soil temperatures. At temperatures near freezing, differences of 2 or 3 C, such as were found in the field, can be critical. Also, *B. tectorum* roots can grow in soil at temperatures as low as 3 C, but the minimum for *A. spicatum* root growth appears to be in the range of 8 to 10 C.

The inherently greater root elongation rate of *B. tectorum* is the key characteristic which accounts for its dominance over *A. spicatum* seedlings. As a result of greater root growth rate and earlier development, *B. tectorum* seedlings usually grow to maturity with roots in a relative abundance of soil moisture. Daubenmire (1959a) proposed that where growth water is not present throughout the summer, the relative rapidity of root penetration is generally the most important factor governing the success of seedlings.

A possible explanation for the rapid elongation rate of *B. tectorum* roots may be found in their cell structure. Not only are these roots smaller in diameter, but cell walls have only a fraction of the thickness observed in *A. spicatum* roots. Assuming an equal rate of photosynthate product in both species, a unit of yield would furnish structural material for at least three to four times as much root length of the *B. tectorum* design. Part of this could be expressed as increased length in the primary root, and part as an extension of secondary branches or adventitious root growth.

*Bromus tectorum* stands maintain a heavy demand on soil moisture stores over a wide range of plant densities. In dense stands, primary and secondary root systems deplete available moisture as they advance. In sparse stands, plants tiller and produce vigorous adventitious roots. These also grow faster during the winter than the primary roots of *A. spicatum*, further depleting the moisture store as they advance.

In the season when growing conditions are favorable for *A. spicatum* seedling growth, *B. tectorum* seedlings already have gained dominance of the site. The extremely diverse root system of *B. tectorum* penetrates practically every pore space in the profile. Moisture content is reduced until relatively high tensions are reached throughout the upper soil horizons. The normally slow rate of *A. spicatum* seedling root growth is further reduced by high moisture tensions.

If the roots upon which an *A. spicatum* seedling depends for water do not reach a dependable moisture supply, it will likely succumb in the summer drought period. It will have performed as if it were a winter



annual. This is the usual fate of *A. spicatum* seedlings growing on sites dominated by *B. tectorum*.

If, on the other hand, an *A. spicatum* seedling succeeds in maintaining life through the first summer drought in a *B. tectorum* stand, it normally faces a long period of suppression. Each successive year *B. tectorum*, capitalizing on winter root growth, robs the upper soil moisture before the principal season of growth occurs in *A. spicatum*. Until a seedling can grow large enough to exert control over *B. tectorum* in its immediate vicinity, it will continue to be suppressed. Mature *A. spicatum* plants exercise control over *B. tectorum* by competition for factors other than soil moisture. The author suspects that reduced amounts of available nitrates is very important.

Growth of either species may be favored in a given year by annual variations in weather. A favorable year for *B. tectorum* is characterized by moist fall and spring weather, combined with normal temperatures. *B. tectorum* growth is limited by delayed fall rains, or dry, cold spring weather. *A. spicatum* growth is enhanced by cool, wet summer weather. In the *B. tectorum* region moist summers are infrequent. In such a season, *A. spicatum* seedlings may become established or previously suppressed older plants may be released to establish dominance.

It is doubtful that *B. tectorum* is forced into early maturity because its roots are shallow, as suggested by Spence (1937). This species probably dries early because its root structure is not conducive to efficient transfer of moisture through heated and dessicated surface soil horizons. The endodermis cells, which in *A. spicatum* are heavily suberized, are thin in *B. tectorum* and apparently offer little resistance to moisture loss. Inability to transfer moisture efficiently becomes progressively more critical in the spring as increasing insolation and rising temperatures accelerate transpiration. Substantiation of these statements lies in (1) examination of *B. tectorum* root transections, (2) discovery that roots of mature, dry *B. tectorum* plants inhabit deep soil layers where there is abundant available moisture, and (3) the fact that *B. tectorum* plants continue to live through the summer season in the occasional situation when surface moisture is available.

Competition for light does not seem to be an important factor between these two species. *A. spicatum* leaves were taller than *B. tectorum* leaves in the root growth study boxes. Thus, it is difficult to imagine *B. tectorum* leaves shading more than the lower leaves of *A. spicatum*. Competition for light was not evident in *B. tectorum* either, since *B. tectorum* plants produced longer roots and equally tall leaves in competition with *A. spicatum* as in a monospecific stand. Densities in the boxes were equivalent to the average densities of *B. tectorum* found in the field. Light intensities in the growth chambers was considerably less than in open sunshine. In full sunshine, light would be even less a factor of competition.

Yields of *B. tectorum* have been determined as high as 3,461 lb/acre, with average yields equaling those

of perennial grass species (Stewart & Hull 1949, Hull 1949). *B. tectorum* produces these yields very efficiently, using only part of the total water store. This is accomplished by early season growth, when transpiration rates are relatively low. By contrast, rapid *A. spicatum* growth and production occurs during the heat of summer. Wasteful transpiration must accompany summer growth in spite of the anatomical structure in *A. spicatum* leaves which slows water loss. Further, *B. tectorum* has a high efficiency of water use (produced larger yields of top growth per unit of water used) than summer growing perennial grasses (Hull 1963). *A. spicatum* was not compared in Hull's test.

Seedlings of the two species compete with each other over a wide geographic area. Within this area are found landscapes with considerable variation in physical features, including soil texture and development, topography, amount and distribution of precipitation, temperatures, and wind. The competitive advantage which *B. tectorum* enjoys over *A. spicatum* seedlings is great enough to overcome much of the natural variation found in semi-arid grassland and sagebrush sites of the Intermountain and Columbia Basin regions. This is evidenced by the general dominance of *B. tectorum* on disturbed sites throughout these regions.

However, a change in one factor, the amount of summer precipitation, reduces *B. tectorum* to an unimportant position as a competitor. Early phenology is not critical where a continuously renewed supply of summer moisture is available. In the moist grassland (*Festucatum*) of eastern Washington for example, *B. tectorum* is a poor competitor, being relegated to occupation of recently disturbed spots (Daubenmire 1942, p. 76). It has a similar place in the great plains, where summer precipitation is the normal pattern.

The selection of *A. spicatum* ecotypes which could successfully compete with *B. tectorum* has been suggested. The selection of an early developing variant, if available, would likely not solve the problem. First, one of the major disadvantages of *B. tectorum* as a forage plant is its early maturity. There would be little point in encouraging the replacement of *B. tectorum* by an *A. spicatum* ecotype which matured as early as the *B. tectorum*. And second, it is unlikely that there is any ecotype available which would come near being as early phenologically as *B. tectorum*. Selection of *A. spicatum* ecotypes for ability of roots to grow rapidly at low temperatures appears more realistic. If one could be found which grows fast enough to at least maintain the tips of its roots in contact with the upper fringe of available soil moisture in a *B. tectorum* stand, it may be able to survive the critical first summer, growing on deep moisture remaining after *B. tectorum* has matured.

#### SUMMARY

*Agropyron spicatum* was a major species dominating millions of acres of the northern intermountain



region in its pristine condition. The introduction of European culture with new use-patterns upset this balance and introduced *Bromus tectorum*, a winter annual which soon displaced *A. spicatum* over wide areas. Serious attempts are now being made to restore perennial grasses to the range. *B. tectorum* competition provides a major barrier to the establishment of seedlings. An understanding of the basic factors controlling competition between these two species will contribute to more successful action programs.

Field experiments to investigate this problem have been conducted at the Harder Ranch site, located near Benge, Washington, and at the Pullman Nursery, on the Washington State University campus at Pullman. Additional studies have been conducted in the laboratory.

Twenty acres of deteriorated range land, on which *B. tectorum* had been controlled with variable success, was seeded to *A. spicatum* in the fall of 1959. In the spring of 1960 a series of plots was established here to study the influence of *B. tectorum* competition (dense, moderate, sparse) upon *A. spicatum* seedlings survival. October, 1960, counts indicated averages of survival to be 39, 69, and 86%, respectively. In July 1960, *A. spicatum* seedlings growing in sparse *B. tectorum* averaged 9.1 and 7.5 times as heavy (green and dry weight, respectively) as *A. spicatum* seedlings growing in dense *B. tectorum*. Moisture lost upon oven drying amounted to 43% for *A. spicatum* seedlings growing in sparse *B. tectorum* and only 16% for *A. spicatum* seedlings growing in dense *B. tectorum*. Soil moisture determinations made on July 25, 1960, when the above-described leaf samples were taken, indicated available moisture was present at depths where roots of the larger plants were growing in sparse *B. tectorum* but none at depths where roots of the smaller plants were growing in dense *B. tectorum*. Soil moisture was available at the lower rooting levels of *B. tectorum* even after this species had matured and died.

*Agropyron spicatum* seedlings growing in sparse *B. tectorum* rooted to an average depth of 95 cm, with maximum penetration to 136 cm. In dense *B. tectorum*, *A. spicatum* seedling roots reached depths of 50 to 60 cm. *B. tectorum* seedlings penetrated to an average depth of 105 cm.

Both species initially produce a primary root system, and if site factors permit, later produce extensive adventitious roots. The adventitious roots of *A. spicatum* grow out laterally from the root crown for a distance of 20 to 30 cm before turning downward. The primary systems of both species, and the adventitious roots of *B. tectorum* grow directly downward from the root crown. *B. tectorum* roots are more finely divided, and make fuller contact with the soil than do *A. spicatum* roots. On the other hand, *A. spicatum* roots are constructed more heavily, and are better adapted to withstand summer drought.

Tests indicate that both species germinate at approximately the same time during moist fall weather.

*B. tectorum* seed germinated more rapidly than *A. spicatum* seed at 10 C, but the reverse was true at 30 C. The two species did not germinate differently at water potentials of 0, 6.2, and 11.4 atm.

Seasonal root growth patterns were studied by use of glass tubes filled with soil and set into the ground in orchard auger holes.

Following field germination in October, *B. tectorum* roots continued to grow throughout the winter. They had reached average depths of 87 cm by March 9. Numbers of leaves, stems, and roots increased continuously throughout the winter also. In contrast, *A. spicatum* roots grew but little during the winter, reaching only 14 cm depth by March 9. Furthermore, numbers of leaves, stems, and roots did not increase as rapidly as in *B. tectorum* during the winter. Winter soil temperatures averaged 1 C at depths where *A. spicatum* root tips were growing and 3 C at deeper levels where *B. tectorum* root tips were growing. *B. tectorum* roots continued to grow at 3 C, but *A. spicatum* roots remained dormant until soil temperatures reached 8 to 10 C in late April. At this time many adventitious roots of *B. tectorum* were at deeper levels than the primary roots of *A. spicatum*. *B. tectorum* seed matured in mid-May, but *A. spicatum* seed had not matured on July 22 when the trial was terminated.

A laboratory study was made of relative rates of root growth under competition, as well as the soil moisture relationships which prevailed. Soil moisture determinations were made using the gamma ray attenuation technique, and root systems were traced by use of a radioactive isotope of phosphorus. Increasing densities of *B. tectorum* decreased the averaged depth of *A. spicatum* seedling root penetration. *B. tectorum* roots grew deeper with increasing *A. spicatum* densities; this appears to indicate that *B. tectorum* is inhibited more by intraspecific competition than by interspecific competition with *A. spicatum*. *B. tectorum* roots consistently were found in soil containing moisture available at less than 1 atm tension. *A. spicatum* roots, on the other hand, were in soil with water available only at tensions greater than 15 atm.

*Bromus tectorum* outcompetes *A. spicatum* seedlings by extending its roots more rapidly during the winter, thus gaining control of the site before *A. spicatum* seedlings become established. *B. tectorum* matures four to six weeks earlier than *A. spicatum*, placing a major stress on the stored moisture supply prior to the needs of *A. spicatum*. At the later date when *A. spicatum* needs the moisture to survive through the summer, moisture has been exhausted at the levels where *A. spicatum* roots have reached in competition with *B. tectorum*.

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